

SMALL RODENTS (MAMMALIA)
FROM EOCENE DEPOSITS OF
SAN DIEGO COUNTY, CALIFORNIA

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JASON A. LILLEGRAVEN

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ABSTRACT

Four genera (*Microparamys*, *Sciuravus*, *Griphomys*, and *Pareumys*) and seven species of small rodents are discussed from Eocene deposits in two areas of San Diego County, California. Fossils from the greater San Diego area (Friars and Mission Valley formations) suggest an earliest "Uintan" (roughly mid Eocene) age. Specimens from the northwesternmost corner of San Diego County in Camp Pendleton Marine Corps Base (?Santiago Formation) suggest a significantly younger assemblage, time-correlative with the Uintan part of the Sespe Formation of Ventura County, California. *Sciuravus* does not occur in the Pendleton-Sespe localities nor does *Griphomys* in the greater San Diego area. One species (*Griphomys toltecus*) is described as new from Camp Pendleton.

Detailed comparisons of the San Diego fauna with taxa from the Rocky Mountain region suggest that widespread overland dispersal of land vertebrates across western North America was possible during at least some part of the earlier Eocene, even by the rodents for which strong

edaphic controls on range extension might have been expected.

Microparamys sp. cf. *M. minutus* from San Diego cannot be distinguished from *M. minutus* from the Powder Wash Bridgerian section of Utah and cannot be ruled out as an ancestor for *M. tricus* from the Pendleton and Sespe deposits. "*Microparamys* sp. D" from the Sespe is a distinct species but is not here formally named. Deciduous premolars in *Microparamys* and *Sciuravus* may have been retained well into adulthood. "*Sciuravus powayensis*" is probably a complex species that in reality included two extremely closely related species; the complexity is not formalized by a new name. The ancestry of *Griphomys* may lie near *Namatomys fantasma*. Similarity is great between *Pareumys* sp. near *P. grangeri* (considered a cylindrodontid) from San Diego and *Spurimus scotti* (considered an ischyromyid) from Wyoming, thus further suggesting the close phylogenetic affinities of the two families.

INTRODUCTION

Renewed interest in the Eocene land vertebrate history of San Diego County, California, has developed within the past 10 years following the pioneering efforts of Drs. Chester Stock and Robert W. Wilson (see Stock, 1948 for summary of earlier work). The more recent field work has utilized underwater screenwashing techniques on fossiliferous sediment and the result has been a much greater appreciation for the diversity of small vertebrate life in the West Coast during the Eocene. The present paper is one of a continuing series describing the elements of the faunas and it focuses on the known structure, taxonomy, and biogeography of four genera and seven species of small rodents. Other papers recently developed for the study include those by Lillegraven (1976 and In press), Lillegraven and Wilson (1975), Lillegraven and McKenna (MS), Novacek (1973, 1976, and In press), Schatzinger (1975), Schiebout (MS), Golz (1976), and Golz and Lille-

graven (In press). A complete bibliography of original research on southern California Eocene land vertebrates along with faunal lists for all known localities is provided by Golz and Lillegraven (In press).

Two general geographic areas are studied in the present paper, one in and around the city of San Diego and the other in the northwesternmost corner of San Diego County in Camp Pendleton Marine Corps Base.

METHODS OF STUDY

Quarrying in the field was followed by a kerosene-to-water washing technique using screen-bottomed boxes with spaces between the wires of 0.75 mm.

Measurements are in millimeters and were taken on an Ehrenreich Photo-Optical Industries (EPOI) "Shopscope." Orientations for measure-

ments are specified below within the generic descriptions.

Stratigraphic terminology used for the San Diego area is that of Kennedy and Moore (1971). The general stratigraphic settings for both the San Diego and Camp Pendleton Eocene sections were described by Lillegraven and Wilson (1975, pp. 858-859) and for the Sespe by Golz and Lillegraven (In press). Detailed descriptions of specific localities are on file at the Museum of Paleontology, University of California, Berkeley, and are available to authorized personnel.

ABBREVIATIONS

AMNH, Department of Vertebrate Paleontology, the American Museum of Natural History
LACM(CIT), Section of Vertebrate Paleontology, Natural History Museum of Los Angeles County (specimen and locality numbers from an older California Institute of Technology collection purchased by the LACM)
UCMP, Museum of Paleontology, University of California, Berkeley
UCMP 110230, Specimen number
V-72088, UCMP vertebrate locality number
YPM, Peabody Museum of Natural History, Yale University

A-P, Anteroposterior length
ANT-W, Anterior width of upper cheek teeth
OR, Observed range of variation
POST-W, Posterior width of upper cheek teeth
W, Transverse width
W-TAL, Width of talonid

W-TRI, Width of trigonid
R, Coefficient of correlation
 $SE_{\bar{x}}$, Standard error of mean
SD, Standard deviation
V, Coefficient of variation
 \bar{x} , Mean of sample

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SYSTEMATIC DESCRIPTIONS

CLASS MAMMALIA LINNAEUS, 1758

SUBCLASS THERIA PARKER & HASWELL, 1897

INFRAClass EUTHERIA GILL, 1872

ORDER RODENTIA BOWDITCH, 1821

FAMILY ISCHYROMYIDAE¹ ALSTON, 1876

GENUS *MICROPARAMYS* WOOD, 1959

Two species of *Microparamys* have been recovered from Eocene deposits of San Diego

¹In the sense of Black (1968); includes the Paramyidae and Ischyromyidae of Wood (1955).

County and are described below. Measurements from all specimens of *Microparamys* spp. (tables 1-4) are as follows:

All upper teeth, permanent and deciduous (hypertrophied hypocones ignored)—

A-P, Parallel to an axis aligned through apices of paracone and metacone but measuring greatest length, anterior face to posterior face, of labial half of tooth.

W, Normal to A-P, measuring greatest width, labial face to lingual face, of central part of tooth.

All lower teeth, permanent and deciduous—

A-P, Parallel to an axis aligned from area of hypoconulid through center of valley between protoconid and metaconid, but measuring greatest length of tooth anterior face to posterior face.

W-TRI, Normal to A-P, measuring greatest width of trigonid from labial face to lingual face of tooth.

W-TAL, As above, only for greatest width of talonid.

Microparamys sp. cf. *M. minutus* (Wilson, 1937)
Figures 1-10

Holotype. *Microparamys minutus*: YPM 10730, right mandibular fragment with M₁₋₂.

Type Locality. Exact locality unknown, Bridger Fm., Bridger Basin, Wyoming (Bridgerian).

Referred Specimens from San Diego County. All isolated teeth: 14 DP⁴s, 12 P⁴s, 25 M¹s, 32 M²s, 12 M³s, 6 DP₄s, 20 P₄s, 23 M₁s, 20 M₂s, 14 M₃s. All are UCMP specimens except LACM(CIT) 2195.

Localities in San Diego County. Friars Fm.: LACM(CIT) 249-S, V-6873, V-6882, V-6888, V-68116, V-68118, V-71183, V-72175, V-72177; Mission Valley Fm.: V-71180, V-71211, V-72157, V-72158, V-72176, V-72179, V-73138.

Distribution of Species. Bridgerian: Bridger Fm., Wyoming; Green River Fm., Utah; Pruett Fm., Texas. Uintan: Friars and Mission Valley formations, California.

Description. DP⁴. The labial extreme of the anterior cingulum is flush with the straight labial border of the tooth (fig. 1). The anterior cingulum is an anteroposteriorly extensive shelf, but narrows markedly in the region of the paraconule. It usually continues onto the base of the protocone well past the paraconule as a thin cingulum, but occasionally terminates just lingual to the paraconular area. There is no direct connection via crests to paracone or protocone apices.

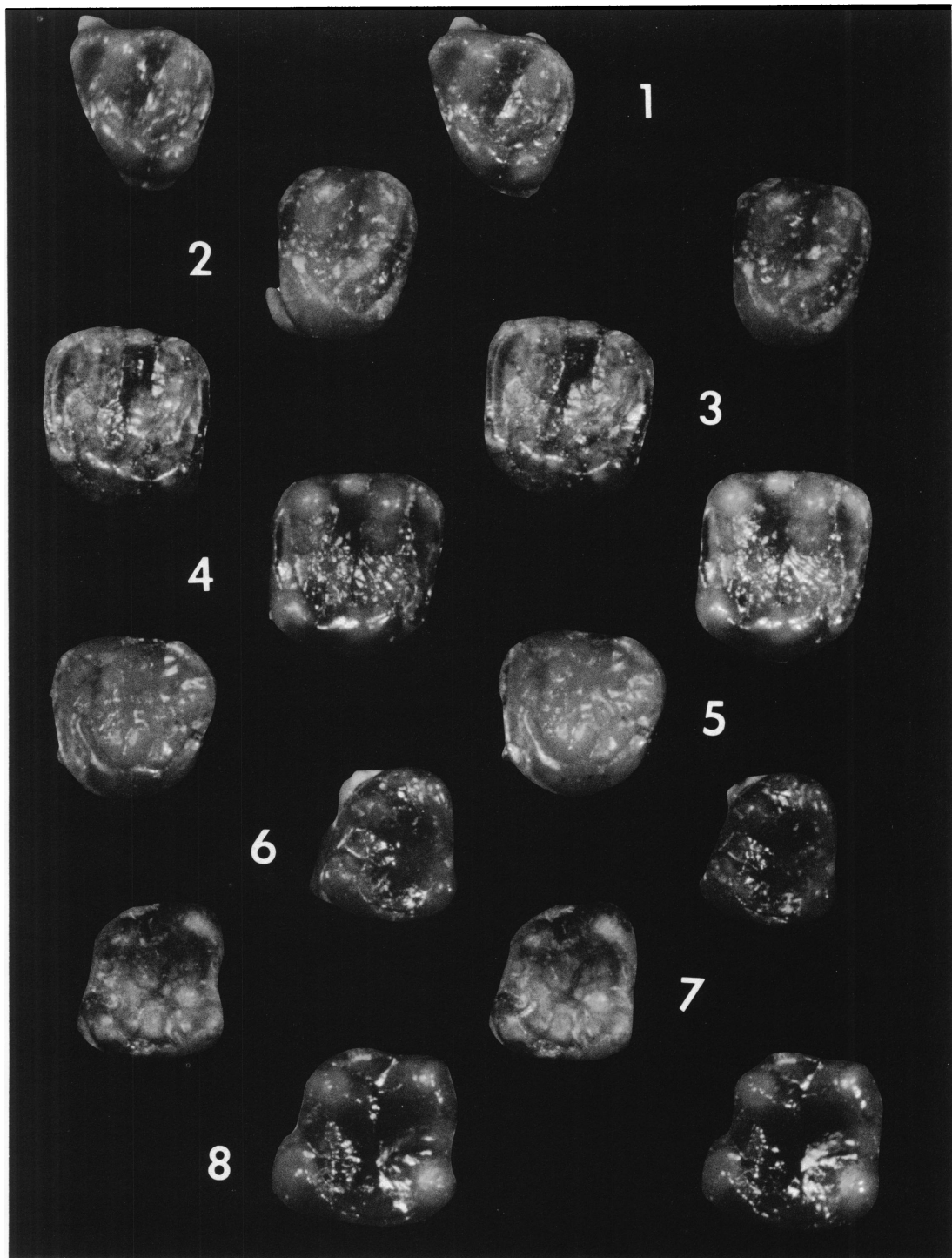
The posterior cingulum is highly variable, but consistently strong. The posterior border runs through most of its length at right angles to the labial edge of the tooth. The labial end usually starts at the posterior base of the metacone, but occasionally (e.g., UCMP 103900) continues

labial to the metacone to join with the mesostyle; all intermediates between these two extremes are present. The lingual end becomes elevated into a distinct hypocone that is connected only at the base with the protocone. The bases of the protocone and hypocone usually extend about the same distance lingually, but on five of 14 specimens the hypocone base extends significantly lingual to that of the protocone. On only three specimens there is a hint of a connecting ridge between the hypocone and metaconule apices.

The paracone is decidedly the tallest of the cusps. It is somewhat compressed anteroposteriorly and has a consistently developed ridge that extends from the apex lingual and somewhat anterior to terminate in an extremely variably developed paraconule. The latter may be conical or ridgelike (with various orientations), distinct or merely a continuation of the paraconal ridge, large or virtually lacking. There is no ridged connection between the paraconule and the rim of the anterior cingulum.

The metacone is also anteroposteriorly compressed. A ridge that is usually continuous extends from its apex to that of the protocone in the following consistent path. It runs straight lingual from the apex of the metacone to the metaconular region, then turns to make a marked convex-anterior sweep that finally terminates at the protoconal apex. The metaconule, like the paraconule, is highly variable. Sometimes it is clearly distinct as a bulbous cuspule, sometimes it is absent, but usually it is little more than a minor swelling and slight elevation of above-described ridge connecting the protoconal and metaconal apices; in two specimens the metaconule is clearly doubled.

The preprotocrista extends anterolabial from the apex of the protocone toward the paraconule from which it is usually separated by a weak depression. No ridges were seen to extend onto the trigon basin from the apex of the protocone. A mesostyle is usually present (absent on two specimens), consistently transversely compressed, and usually rather centrally placed between the paracone and metacone and distinct from both. On two specimens, however, the mesostyles are expansions of a labial cingulum that can extend completely around the labial base of the meta-



FIGS. 1-8. Stereophotographs in occlusal view of isolated cheek teeth of *Microparamys* sp. cf. *M. minutus* (Wilson, 1937) (figs. 1-3 20 \times , figs. 4-6 21 \times , figs. 7, 8 22 \times). 1. UCMP 96462, left DP⁴ from V-71211. 2. UCMP 109501, left P⁴ from V-72157. 3. UCMP 96464, left M¹ from V-71211. 4. UCMP 104169, right M² from V-71211. 5. UCMP 101460, left M³ from V-72158. 6. UCMP 106274, left DP₄ from V-71211. 7. UCMP 99430, left P₄ from V-71183. 8. UCMP 99217, left M₁ from V-71211.

cone to be continuous with the posterior cingulum. There is no ridge extending from the mesostyle linguad onto the trigon basin.

Only about one-third of the specimens show significant degrees of crenulation of the enamel on the occlusal surface of the tooth.

DP⁴s are three-rooted with extremely thin walls. The proto-hypoconal root is nearly twice as long as the enameled crown is high. It is somewhat compressed anteroposteriorly and its base extends from the lingual extreme of the crown to a point almost exactly halfway to the labial edge of the crown. The base of the proto-hypoconal root does not extend so far as the anteriormost extreme of the protocone nor so far as the posteriormost extreme of the hypocone. The paraconal and metaconal roots are smaller in diameter, diagonally compressed, more or less parallel to one another, and curve slightly anterolabial toward their tips. The paraconal root is slightly more robust than the metaconal root and is based dorsal to the entirety of the paracone plus most of the enlarged anterior cingulum.

P⁴. This tooth is shorter anteroposteriorly but wider in absolute measurements (table 1) than DP⁴, thus the former is far more rectangular (fig. 2). The arrangements and characteristics of cusps and ridges, however, are basically the same between the teeth and only significant differences are described here.

The anterior cingulum is much weaker in its

labial half than in DP⁴, being of typical non-shelf-like construction throughout its length. Its labial origin in P⁴ is slightly lingual to the labial edge of the tooth. The lingual extent is usually as in DP⁴, but in two specimens a weak ridge connects the paraconule and the cingulum; in three specimens the lingual termination of the cingulum is at the level of the paraconule. The posterior cingulum is as in DP⁴ except that the hypocone is considerably less hypertrophied and in all cases its labial origin is on the posterior base of the metacone. As in DP⁴, no connections are observed between the hypocone and metaconular region.

The lingual ridge from the apex of the paracone runs more directly linguad than in DP⁴ and makes contact with a minuscule paraconule. The lingual ridge from the apex of the metacone either runs uninterrupted all the way to the protoconal apex or encounters a distinct metaconular region. Metaconules are usually present (absent in only one specimen) and tend to be doubled or even multiplied (e.g., UCMP 109501).

Only one specimen (UCMP 104173) is seen to have a weakly developed ridge that runs from the apex of the protocone labial onto the trigon basin. A mesostyle is usually not present but may be represented by a minuscule elevation of enamel. One specimen (UCMP 99213) has a pair of mesostyles with one set on the posterior base of the paracone and the other on the anterior base

TABLE 1
Standard Statistics for Upper Teeth of *Microparamys* sp. cf. *M. minutus* from
the Greater San Diego Area, California

		N	O.R.	\bar{X}	SE \bar{X}	S.D.	V	R
A-P	DP ⁴	14	0.917-1.175	1.057	0.020	0.076	7.2	—
	P ⁴	11	0.950-1.114	1.035	0.017	0.055	5.4	—
	M ¹	25	1.031-1.329	1.204	0.016	0.079	6.6	—
	M ²	31	1.073-1.364	1.195	0.011	0.063	5.3	—
	M ³	12	1.162-1.317	1.235	0.014	0.048	3.9	—
W	DP ⁴	14	0.978-1.203	1.071	0.015	0.057	5.3	—
	P ⁴	12	1.130-1.364	1.246	0.020	0.069	5.5	—
	M ¹	24	1.171-1.434	1.338	0.015	0.076	5.7	—
	M ²	32	1.192-1.472	1.346	0.012	0.066	4.9	—
	M ³	12	1.107-1.325	1.228	0.017	0.058	4.7	—
A-P/W	DP ⁴	14	0.882-1.055	0.987	0.013	0.049	5.0	0.722
	P ⁴	11	0.750-0.881	0.828	0.012	0.040	4.8	0.615
	M ¹	24	0.837-1.135	0.907	0.012	0.058	6.4	0.486
	M ²	31	0.839-0.958	0.888	0.006	0.032	3.6	0.759
	M ³	12	0.965-1.071	1.235	0.014	0.048	3.9	0.746

of the metacone; a weak ridge runs lingual from each a short distance toward the trigon basin.

The enamel of the occlusal surface of most teeth is slightly crenulated. P^4 s are basically two-rooted with a heavy, somewhat anteroposteriorly compressed proto-hypoconal root that nearly covers the entire base of the crown; a combined paraconal-metaconal root is restricted to the labial fourth of the base of the crown. Both roots are remarkably straight and project directly dorsad from the crown. The tip of the proto-hypoconal root is curved slightly labiad in some. The paraconal-metaconal root is vertically grooved on its labial surface between the paraconal and metaconal parts as though it were "trying" to become two separate roots. In some specimens (e.g., UCMP 110235) the paraconal-metaconal root remains an intact unit all the way to its distal tip. Others, however, have distinctly bifurcated and anteroposteriorly divergent paraconal and metaconal tips (e.g., UCMP 104173). Specimen UCMP 101236 shows a nearly complete separation of paraconal and metaconal parts of the root. The dentinal walls of the roots are much thicker than those seen in DP^4 .

M^{1-2} . These teeth are difficult to differentiate with certainty (figs. 3, 4). However, it is generally the case among primitive rodents that in going from M^1 to M^2 the following changes occur: (1) The height of the metacone and size of metacone region decreases relative to the paracone; (2) the teeth become proportionally shorter anteroposteriorly and wider transversely; and (3) the importance of the hypocone decreases slightly. When the isolated upper molars were sorted according to those criteria, most teeth divided into two groups of roughly equal numbers that I here consider to be M^1 s and M^2 s. A number of specimens (perhaps 10% or so), however, are structurally intermediate and likely have been misidentified in this study leading to some inaccuracy in the statistics in table 1. The morphologies and sizes are so similar between the two teeth, however, that I do not consider the probable errors to be particularly serious.

M^{1-2} are described together. The teeth are considerably longer and wider in absolute measurements than P^4 with a much more quadrangular appearance when seen in occlusal view. The anterior cingulum is prominent and rather

uniform in anteroposterior width throughout its extent. Its points of origin and termination are consistent in respectively being the anterolabial corner of the base of the paracone and on the anterior base of the protocone just lingual to the paraconular region. Only in one specimen (UCMP 110048, an M^2) is there a direct connecting crest between the paraconular region and the anterior border of the anterior cingulum. Several specimens, however, show the incipient development of such a crest by an anterior bulging of the paraconular region.

Both the paracone and metacone are markedly anteroposteriorly compressed and have crests running more or less continuously to the protoconal apex. Paraconules as such are minuscule (e.g., UCMP 96309) and seen only in unworn teeth if present at all. I would estimate their presence in only about 30 percent of the specimens. Metaconules are usually present (about 80% occurrence) but are usually little more than a minor expansion of the ridge to the protocone. When present, the metaconules are almost invariably single, but were doubled but extremely small in two M^2 s (e.g., UCMP 101262). The metaconular area is usually continuous via a crest with the apex of the protocone (M^1 s 67%, M^2 s 87%) but occasionally is also connected via a weak crest with the hypocone base (18% M^1 s, 10% M^2 s). In 15 percent of the M^1 s the metaconular area is connected by crests neither to the protocone nor to the hypocone (condition not observed in M^2 s) and in a single specimen of M^2 (UCMP 100033) a crest extends from the metaconule to the hypocone without any connection to the protocone. A number of other specimens showed hints at this "hypoconal capture" of the metaconular region by opposed expansions of either the hypocone or the metaconule or both. Roughly 60 percent of the specimens (e.g., UCMP 109941) showed a weakly developed spur analogous to a premetaconular wing projecting anterolabiad from the metaconular region.

A mesostyle is universally present and more or less centrally placed between the bases of the paracone and metacone on the labial margin of the tooth. It is doubled on roughly 10 percent of the individuals (e.g., UCMP 101661). A low ridge running lingual a short distance from the apex of

the mesostyle is commonly present (45% M^1 s, 70% M^2 s) and on at least two specimens two parallel ridges leave from a single mesostyle (e.g., UCMP 101160).

The hypocone is well developed as the expanded conical terminus of the posterior cingulum. Although not so long anteroposteriorly as the protocone, the two cusps are usually about equal in height. The strong posterior cingulum consistently makes its origin on the posterolingual base of the metacone.

The protocone usually (60% M^1 s, 75% M^2 s) has an incomplete ridge extending posteriad from its apex toward the hypoconal base; it is nearly complete in UCMP 106284. On the remaining specimens the ridge is lacking and the posterior surface of the protocone is broadly rounded. Yet another ridge commonly (45% M^1 s, 63% M^2 s) extends labiad onto the floor of the trigon basin from the apex of the protocone. The ridge is usually low and only rarely is strongly conspicuous.

Almost all upper molars (M^3 included) have slightly crenulated enamel on the occlusal surfaces. Less than 10 percent are uncrenulated and the degree of crenulation is strong (e.g., UCMP 104169) in less than 20 percent of the specimens.

The proto-hypoconal root of M^{1-2} is robustly rounded in cross section and less than twice as long as the height of the crown. It directly supports the protocone and only the anterior base of the hypocone; the root underlies less than half of the transverse width of the crown. A rugose expansion of the tip of the proto-hypoconal root is occasionally developed (e.g., UCMP 101184) and frequently the tip curves somewhat labiad. The paraconal and metaconal roots are fully distinct and are much less strongly developed. They vary from having circular cross sections to being markedly compressed diagonally. The paraconal root is usually slightly greater in diameter than the metaconal root. The paraconal root usually courses straight dorsad from the base of the crown, but the metaconal root commonly projects markedly posteriad from the crown. The labial roots are considerably shorter than the proto-hypoconal root, being only a bit longer than the enamel crown height.

M^3 . This tooth is structurally greatly sim-

plified compared with M^{1-2} (fig. 5). A metacone, distinct hypocone, and recognizable paraconule are lacking. A mesostyle is present in only seven of 12 available specimens and when present, only two of five specimens show a lingually directed spur. A metaconule as such is unrepresented other than by the slightest thickening of the postprotocrista just posterior to the center of the occlusal surface of the tooth; short spurs commonly diverge in various directions from that point. The anterior cingulum is as in M^{1-2} and also lacks any ridged connection with the paraconular area. A low ridge extending labiad onto the trigon basin from the apex of the protocone is seen in five of 12 specimens. The posterior cingulum is greatly expanded posteriorly as a broad shelf through its labial half. It then narrows rapidly through its lingual half to become a ridge that ends variously at the apex of the protocone, the base of the protocone, or, following a sharp labial turn, in the metaconular region. The last part of this ridge is usually slightly expanded but a distinct hypocone in the sense of M^{1-2} is certainly not developed.

The crenulations on the occlusal surface of M^3 are generally more pronounced than on M^{1-2} and are especially prominent in two areas of the tooth. These are: (1) On the expanded shelf of the posterior cingulum with the crenulations running roughly anteriad from the back rim; and (2) from various parts of the preprotocristae and postprotocristae with the crenulations converging on the center of the trigon basin.

The three roots of M^3 are quite variable, but consistently shorter, less robustly developed, and more likely to be curved along their length than those seen in M^{1-2} . As in M^{1-2} , the protoconal root is the longest and the greatest in girth, but the paraconal root is greatly reduced, being little more than an elongated spike of dentine in some cases (e.g., UCMP 106413). The third root that underlies the greatly expanded labial part of the posterior cingulum is nearly as large as the protoconal root in some cases. Usually, however, the cingular root is intermediate in size between the other two. The protoconal and cingular roots are usually set closely to one another and the latter is well separated from the paraconal root.

DP₄. Teeth identified as DP₄s of *Microparamys* sp. cf. *M. minutus* (fig. 5) are struc-

turally remarkably variable. All teeth, however, have a distinct mesoconid plus other features characteristic of *Microparamys* and it is unlikely that the sample includes deciduous teeth of other taxa.

An anteroconid is present on four of the six available specimens and varies from a tiny stylid to a cuspule nearly as large as the protoconid. It is developed as a distinct cuspule on three of the specimens, but is set on a short anterior cingulum extending from the apex of the metaconid on the fourth. The anteroconid is the most anterior elevation on the tooth and its apex is set at the transverse center of the crown. An anterior cingulum is present on only one specimen, its labial

end is not expanded, and it does not make contact with the base of the protoconid.

The protoconid is always present but highly variable in size. Three of the six specimens have a weak protoconid much smaller than the metaconid and set well posterior to it. The other three, however, show progressively stronger development of the protoconid and in UCMP 109787 it is nearly equal in height and girth with the metaconid and is set only slightly posterior to it. A postprotocristid is lacking as a distinct crest, but a weakly raised line of enamel usually unites the bases of the protoconid and the metaconid.

The posterior cingulum extends continuously

TABLE 2
Standard Statistics for Lower Teeth of *Microparamys* sp. cf. *M. minutus* from the Greater San Diego Area, California

		N	O.R.	\bar{X}	$SE_{\bar{X}}$	S.D.	V	R
A-P	DP ₄	6	1.117-1.218	1.164	0.014	0.035	3.0	—
	P ₄	20	0.940-1.326	1.089	0.021	0.095	8.7	—
	M ₁	22	1.119-1.344	1.233	0.015	0.069	5.6	—
	M ₂	20	1.122-1.416	1.260	0.014	0.063	5.0	—
	M ₃	13	1.178-1.493	1.333	0.019	0.068	5.1	—
W-TRI	DP ₄	6	0.697-0.952	0.787	0.036	0.089	11.3	—
	P ₄	20	0.640-1.121	0.856	0.026	0.116	13.6	—
	M ₁	22	0.990-1.276	1.103	0.015	0.068	6.2	—
	M ₂	20	1.028-1.427	1.167	0.021	0.096	8.2	—
	M ₃	18	1.057-1.275	1.183	0.017	0.063	5.3	—
W-TAL	DP ₄	6	0.921-1.117	0.983	0.028	0.069	7.0	—
	P ₄	20	0.892-1.250	1.032	0.021	0.093	9.0	—
	M ₁	22	1.103-1.455	1.250	0.018	0.084	6.7	—
	M ₂	20	1.130-1.405	1.248	0.015	0.069	5.5	—
	M ₃	13	1.081-1.270	1.180	0.018	0.066	5.6	—
A-P/W-TRI	DP ₄	6	1.230-1.693	1.494	0.066	0.162	10.9	-0.014
	P ₄	20	1.145-1.602	1.288	0.026	0.115	8.9	0.849
	M ₁	22	1.006-1.217	1.119	0.013	0.060	5.3	0.604
	M ₂	20	0.992-1.218	1.084	0.013	0.058	5.3	0.782
	M ₃	13	1.032-1.222	1.128	0.016	0.056	5.0	0.557
A-P/W-TAL	DP ₄	6	1.048-1.260	1.188	0.033	0.080	6.7	0.143
	P ₄	20	0.956-1.149	1.056	0.011	0.050	4.8	0.862
	M ₁	22	0.901-1.151	0.993	0.012	0.058	5.9	0.668
	M ₂	20	0.950-1.075	1.011	0.008	0.037	3.6	0.770
	M ₃	13	1.067-1.195	1.131	0.013	0.046	4.1	0.713
W-TRI/W-TAL	DP ₄	6	0.734-0.852	0.799	0.016	0.040	5.0	0.946
	P ₄	20	0.717-0.960	0.834	0.016	0.070	8.4	0.837
	M ₁	22	0.828-0.943	0.883	0.004	0.020	2.3	0.916
	M ₂	20	0.878-1.016	0.934	0.008	0.034	3.6	0.924
	M ₃	13	0.960-1.056	1.004	0.008	0.028	2.8	0.878

from the apex of the hypoconid to the apex of the entoconid. There is no development of a hypolophid. A sign of a hypoconulid is lacking in one specimen, but on the other five it is represented by a minor expansion of the posterior cingulum (three specimens) or by a clearly distinct anteroposteriorly compressed cuspule (e.g., UCMP 109787).

Crenulations are usually weakly developed on the occlusal surfaces of DP₄s.

No specimens of DP₄ with complete roots have yet been recovered. As shown by UCMP 106274 and UCMP 106614 (*Microparamys tricus*), however, the teeth are two-rooted with extremely thin dentinal walls. The anterior root projects straight ventrad or perhaps slightly anteroventrad, whereas the posterior root projects markedly posteroventrad at an angle of about 45 degrees from the occlusal surface of the tooth.

P₄. An anteroconid is developed on only six of the 20 available specimens. In all cases the cuspule is weakly developed as an elevation distinct from the metaconid (fig. 7). The anteroconid, in contrast to DP₄, is usually slightly posterior to the anteriormost part of the crown which is the base of the metaconid. An anterior cingulum is present on only three of the specimens. It lacks a labial expansion and usually closes against the protoconid base. The cingulum is short, low, and does not make contact with the metaconid apex.

The protoconid may be absent (two specimens) but usually is present. When present, it varies in size from a low weak cuspule (roughly nine specimens) through a graded series to cusps nearly as tall and robust as the metaconid. A clearly distinct postprotocristid is usually absent other than a weakly developed elevation curving in a convex-posterior arc toward the posterolabial base of the metaconid. In two specimens the postprotocristid is slightly stronger and projects as a spur toward the region of the metastylid.

A metastylid is usually lacking (14 of 19 specimens). Most commonly the posterolingual edge of the metaconid is elongated posteriad into a ridge that may or may not have a minor expansion or elevation in the region expected for a

metastylid. In the five specimens possessing a metastylid it is always weak and single.

A hypoconulid is absent in eight of 19 specimens, represented as a mere expansion of the posterior cingulum in eight specimens, and present as a small but clearly distinct cuspule in three. When present, it forms the posteriormost part of the crown and is almost perfectly equidistant between the apices of the entoconid and hypoconid.

The posterior cingulum has two common modes of development. In 10 of 19 specimens it forms a continuous ridge sweeping in a convex-posterior arc from the apex of the hypoconid to the apex of the entoconid; no hypolophid is developed from the entoconid. The remaining specimens, however, develop the posterior cingulum only from the hypoconid to the region of the hypoconulid and the connection between the entoconid and the hypoconulid is made by a hypolophid. When the latter occurs, a weak continuation of the posterior cingulum dives ventrolingual down the posterior surface of the tooth from the hypoconulid (e.g., UCMP 110246).

A mesoconid is present and although the ectolophid is usually continuous from the mesoconid to the protoconid and hypoconid bases, four of the specimens show deep transverse valleys anterior and posterior to the mesoconid (e.g., UCMP 101558). Only rarely does a spur progress lingual onto the trigonid basin from the mesoconid (e.g., UCMP 109505).

Usually the occlusal surfaces lack crenulation (10 of 20 specimens) or have only a slight degree of crenulation (9). One specimen (UCMP 101691) is rather heavily crenulated.

The two roots of P₄ are about equal in length and are more than twice as long as the crown is high. The talonid root is the more robust. It is moderately compressed anteroposteriorly and its length is usually somewhat concave posteriorly. The root projects straight ventrad or slightly posteroventrad from the crown. The trigonid root is much more slender throughout its length and is usually nearly circular in cross section. The root is usually slightly convex anteriorly and projects slightly mediad in comparison with the path of the talonid root.

M_{1-2} . The lower molars (figs. 8, 9) lack an anteroconid as such, but a well-developed anterior cingulum (anterolophid of Wood, 1962) begins at the apex of the metaconid, dives quickly down the anterolabial face of the metaconid to continue labiad along the anterior border of the tooth to terminate well short of its labial edge. The labial third of the cingulum commonly is weakly expanded anteroposteriorly and raised slightly in elevation, but certainly is not bulbous. A slight gap usually tends to separate the enlarged area from the more lingual part of the cingulum, but such a gap is sometimes lacking. There is always a distinct separation between the labial terminus of the cingulum and the anterior base of the protoconid, but the gap is generally narrower in M_2 s than in M_1 s.

The protoconid is much smaller and lower than the metaconid and is usually somewhat compressed anteroposteriorly. A postprotocristid (metalophulid II of Wood and Wilson, 1936) is universally present that initially projects straight linguad from the apex of the protoconid then proceeds in one of two distinct courses. In M_1 s the postprotocristid usually (16 of 22 teeth) runs directly toward the metaconid, either as a straight crest or in the form of a convex-posterior arc. Only in four of these 16 specimens, however, does the postprotocristid run as a continuous ridge up the posterolabial face of the metaconid to its apex. The remaining 12 specimens have a distinct gap in the ridge at the valley between the bases of the protoconid and metaconid. In all 12 specimens, however, the postprotocristid continues again after the gap up the face of the metaconid to its apex. Six of the available 22 specimens of M_1 have the alternate course for the postprotocristid which is to run for a short distance in the direction of the region of the metastylid rather than to the metaconid. The latter condition has been observed only in M_1 s with no such alternate path in M_2 s. There is no sign of a posterolabial ridge on the face of the metaconid in these peculiar variants of M_1 , thus the cusp has a markedly more concave posterolabial face.

Metastylids are only rarely present as distinct cusps (two of 22 M_1 s, e.g., UCMP 104170, no M_2 s). Usually there is only the slightest hint of a metastylid expansion on the posteriorly extending ridge from the metaconid.

A hypolophid is not present except as only

the slightest hint of a ridge extending labiad onto the talonid basin from the apex of the entoconid in four of 22 available M_1 s (e.g., UCMP 104170) and in UCMP 96467, a M_1 that has a weak hypolophid extending, as in some P_4 s, from the apex of the entoconid to the hypoconular region.

The posterior cingulum is complete and uninterrupted in its convex-posterior course from the apex of the hypoconid to the posterior base of the entoconid. There is no definitive hypoconulid other than the slightest of expansions of the posterior cingulum in the appropriate area; commonly there is not the slightest trace of a hypoconulid.

A mesoconid is universally present and the ectolophid is usually complete fore and aft from the mesoconid. About 25 percent of the time, however, a deep transverse gap separates the mesoconid from its surrounding cusps, especially from the protoconid. Usually there are no spurs extending mediad from the mesoconid, but such are occasionally seen (e.g., UCMP 96496).

Crenulation is present but slight on the occlusal surfaces of most M_{1-2} s but becomes rather strong in roughly 20 percent of the teeth. Only rarely are no crenulations present.

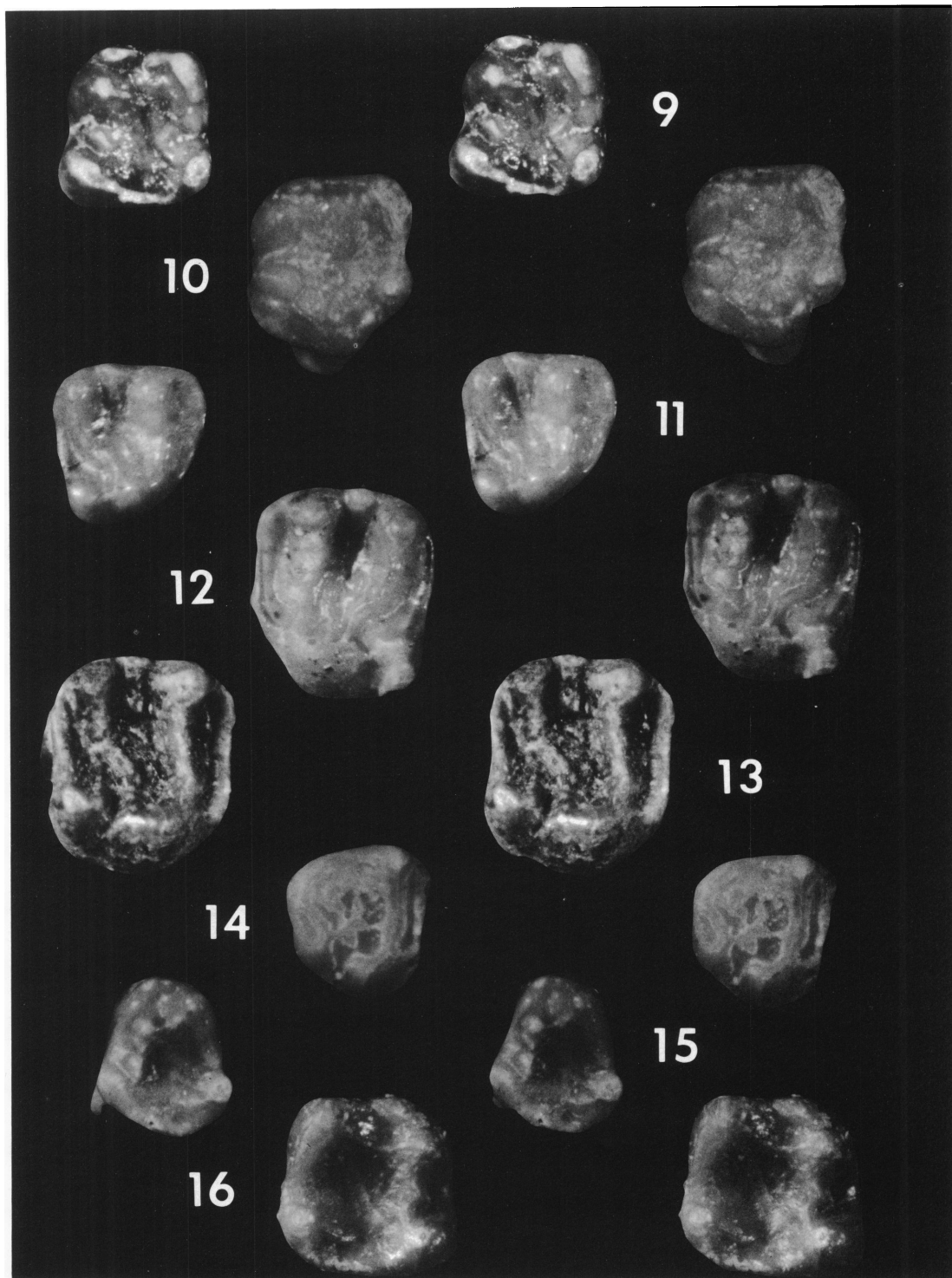
The double roots of M_{1-2} are basically like those of P_4 except that the molar roots tend to be a bit shorter and vastly more compressed anteroposteriorly; the compression is particularly striking on the trigonid root. The molar roots are also much straighter than are those of P_4 and the trigonid and talonid roots are occasionally slightly concave anteriorly and posteriorly respectively, exactly opposite the condition of P_4 .

M_3 . Most of the features and variations seen in M_{1-2} are also present in M_3 ; thus the following description summarizes only the differences characteristic of M_3 .

The labial extreme of the anterior cingulum is set much more closely to the anterior base of the protoconid than in M_{1-2} and in most cases physical contact is made (fig. 10). There is also virtually no expansion of the labial one-third of the cingulum.

The postprotocristid is generally shorter than its homologue in M_{1-2} in that it almost always stops well short of the posterolabial face of the metaconid. There is also no ridge on the concave posterolabial face of the metaconid in contrast to the usual condition in M_{1-2} .

The posterior cingulum is usually not com-



FIGS. 9, 10. Stereophotographs in occlusal view of isolated left cheek teeth of *Microparamys* sp. cf. *M. minutus* (Wilson, 1937) (21 \times). 9. UCMP 96479, M₂ from V-71211. 10. UCMP 106842, M₃ from V-72157.

FIGS. 11-16. Stereophotographs in occlusal view of isolated cheek teeth of *Microparamys tricus* (Wilson, 1940a) from V-72088 (figs. 11, 12 18 \times , figs. 13-16 17 \times). 11. UCMP 101916, right DP⁴. 12. UCMP 110359, left M¹. 13. UCMP 106683, right M². 14. UCMP 104129, right M³. 15. UCMP 106614, left DP₄. 16. UCMP 99356, right M₁.

plete from the hypoconid to the entoconid, and usually terminates in an expanded hypoconulid area. A pronounced bight is seen in occlusal view on the posterolingual corner of the tooth between the expanded hypoconulid and the entoconid. The length of M_3 is greatest (table 2) within the tooth series mainly because of the hypertrophied hypoconulid region.

The degree of crenulation in most specimens is greater than in M_{1-2} .

The roots of M_3 are considerably shorter than those of M_{1-2} . The talonid root is nearly circular in cross section, it projects posteroventrad, and is significantly longer than the trigonid root. The trigonid root is extremely compressed anteroposteriorly but is slightly wider transversely than the talonid root. The trigonid root projects slightly posteroventrad.

Discussion. The available specimens from the greater San Diego area show all the features defined by Wood (1962, p. 158) as characteristic of the genus *Microparamys* and indicate the greatest similarity with *M. minutus*. The holotype of *Microparamys minutus* (Wilson, 1937) was collected from an unknown locality somewhere within the Bridger Basin of Wyoming from sediments of Bridgerian age (Wilson, 1937). The description of the type specimen follows in most respects the morphology of those from the San Diego area. The only significant difference is that the Bridgerian specimens have "more or less distinct metastylids . . ." (Wilson, 1937, p. 454) on the lower molars, whereas such structures are present on only two of 44 specimens from San Diego. With respect to size, however, all measurements of M_2 of the holotype (Wilson, 1937, p. 455) exceed the range of variation seen in the West Coast specimens and those of M_1 of the holotype are at or very close to the upper extremes (table 2). Thus secure identification to the species level of the San Diego material may never be possible because of the nature of the data associated with the type.

Dawson (1968, pp. 334-341) described a series of teeth from Powder Wash of the Bridgerian part of the Green River Formation in north-eastern Utah and referred them to *Microparamys minutus* although she did observe some differences from the type and paratypic material. The descriptions of the Powder Wash material follow in all respects the morphology of the San

Diego specimens and only five of 54 measurements listed by Dawson (1968, table 3) fall outside the observed ranges of the West Coast specimens (tables 1, 2). I believe the Powder Wash and San Diego animals represent conspecifics using available morphological and morphometric criteria; they cannot be distinguished except by stratigraphic and geographic occurrence. How this species is related to that represented by the type of *M. minutus*, however, is quite another problem.

I agree completely with Wood (1962, p. 165) that the two teeth from the Uintan Tapo Ranch locality of the Sespe Formation of California identified by Wilson (1940a, p. 72) as "*Microparamys* [*Paramys*] cf. *minutus*" are distinct from that species. Wood (1962, p. 165) referred to the teeth as representing "*Microparamys* sp. D." Although it is clearly distinct at the species level from *M. minutus*, a new trivial name should probably not be coined until the hypodigm increases thus allowing a more thorough diagnosis. The significant differences seen in M_2^2 of the Sespe from those from San Diego are as follows: (1) Larger size (table 3) as measurements fall two to five standard deviations above the mean and outside the range of variation in all measurements but one (compare with tables 1 and 2); (2) M_2 has a strongly developed hypolophid that runs posterolabial from the apex of the entoconid toward, but stopping short of, the hypoconular area (structure of this orientation seen weakly developed only in a single San Diego specimen); (3) M^2 has a well-developed ridge between the paraconular region and the rim of the anterior cingulum (seen in only one San Diego specimen); (4) M^2 lacks a mesostyle (universally present in San Diego specimens); (5) a labially directed ridge from the apex of the protocone onto the trigon basin is strongly developed on M^2 (it is absent in nearly half of the San Diego specimens and when present is weak); (6) the ridge between the metaconular region and the protoconal apex is broken (the crest is complete in nearly 90% of the San Diego specimens); and (7) a strong ridge connection exists between the anterior end of the hypocone and the metaconular area (incipient tendencies toward this condition are seen in only a few San Diego specimens). The sample size of the San Diego material is large enough to lend some confidence to the reality of

the distinctions listed above. Also, the differences seen in *Microparamys* sp. D are advancements over the more primitive conditions seen in *M. minutus*.

Wood (1962, p. 158) provided a synopsis of dental evolutionary trends within the genus. Teeth in the San Diego sample seem to be quite primitive with regard to these trends in that: (1) A hypoconulid is absent other than an occasional minor expansion of the posterior cingulum in the appropriate area; (2) the postprotocristid is usually incomplete to the metaconid such that the trigonid and talonid basins are incompletely separated; (3) the hypocone is separated from the metaconular region and the connection is complete between the apices of the metaconule and protocone; and (4) the degree of crenulation is usually weak except in M_3^3 . The specimens are advanced, however, in that the gap between the labial terminus of the anterior cingulum (anterolophid of Wood, 1962) and the protoconid is well developed, especially in M_1 . The labial terminus of the anterior cingulum is usually not particularly cusped as seen in presumably still more advanced later Uintan specimens of *Microparamys dubius* (Wood, 1949) (described by Dawson, 1966, pp. 100-101).

Rodent specimens referable or very close to *Microparamys minutus* are geographically widespread in North America, now having been recovered from Wyoming, Utah, California, and southwestern Texas (Wood, 1973). Only those from California have been recovered from sediments characterized by a Uintan fauna; all others are from supposedly Bridgerian deposits. The San Diego specimens are so similar to those of the well-described Bridgerian Powder Wash sample

(see Dawson, 1968) that I see no justification in assigning the material to the less well-known *M. dubius* from the Uintan of Wyoming (see Dawson, 1966 and 1974). The morphological level of advancement of the San Diego sample on all available criteria seems to be characteristic of a late Bridgerian or early Uintan stage.

The tiny isolated lower molar (LACM [CIT] 2195) mentioned by Wilson (1940a, p. 83) came from what is now called the Friars Formation (loc. LACM [CIT] 249-S) and follows in all respects the description of *Microparamys* sp. cf. *M. minutus* of the present paper.

It was initially surprising to me to find the high number of deciduous premolars in proportion to the number of permanent P_4^4 s (e.g., 14 DP^4 s vs. 12 P^4 s). After checking a wide variety of genera of modern sciurids, however, it was noted that deciduous teeth among this group are commonly retained well into adult life and the permanent molars may be significantly worn before permanent P_4^4 s are emplaced. The same may have been the case with *Microparamys* in the Eocene. Other possibilities for the high proportion of deciduous teeth exist, of course, and include high differential mortality of juveniles and/or some peculiarity of the habitat that favored preservation of juveniles. Only the collection of a series of jaws will solve the problem.

Microparamys tricus (Wilson, 1940a)
Figures 11-16

Holotype. LACM(CIT) 1122, right mandible with $I_1 P_4 M_{1-3}$.

Type Locality. LACM(CIT) 150, Pearson Ranch, Uintan part of Sespe Formation, Ventura County, California.

TABLE 3
Measurements and Ratios of Upper and Lower Molars of "*Microparamys* species D"
from Locality LACM(CIT) 180, Ventura County, California

			A-P	W	$\frac{A-P}{W}$			
M^2	LACM(CIT)	2155	1.386	1.725	0.803			
						$\frac{A-P}{W-TRI}$	$\frac{A-P}{W-TAL}$	$\frac{W-TRI}{W-TAL}$
M_2	LACM(CIT)	2156	1.438	1.422	1.492	1.011	0.964	0.953

Referred Specimens from San Diego County. All isolated teeth. DP⁴, 101916; M¹s, 102003, 110359; M²s, 101981, 106683; M³, 104129; DP₄, 106614; P₄, 101953; M₁s, 99356, 106499 (all UCMP specimens).

Locality in San Diego County. UCMP V-72088, ?Santiago Formation, Camp San Onofre, Camp Pendleton Marine Corps Base.

Distribution of Species. Sespe and ?Santiago formations (Uintan), California.

Comments and Comparisons. A series of 10 isolated teeth of a species of *Microparamys* was recovered from Uintan deposits in the northern end of Camp Pendleton Marine Corps Base in northernmost San Diego County (see Lillegraven and Wilson, 1975, p. 858 for discussion of locality). The teeth are indistinguishable morphologically from those of *M. tricus* of the Sespe Formation in Ventura County. The teeth from V-72088 are consistently slightly smaller than the Sespe specimens (table 4). However, because of the small sample size the significance of the

differences (i.e., phylogenetic or due to individual variation) cannot yet be determined. Except for their much larger size, the teeth for the species are like those described above for *M. sp. cf. M. minutus* and only the differences within each tooth of the dental series are telegraphically enumerated below. These differences can act as a revised diagnosis of the species. The roots of the teeth are as described above for *M. sp. cf. M. minutus*.

DP⁴ (fig. 11) as in *M. sp. cf. M. minutus* except: (1) base of hypocone projects farther lingually than base of protocone (also seen in *M. sp. cf. M. minutus*, but as uncommon condition); (2) mesostyle more rounded (generally more compressed transversely in *M. sp. cf. M. minutus*), with weak ridges extending linguad onto trigonid basin (ridges absent in *M. sp. cf. M. minutus*); (3) weak ridge extends from apex of protocone labiad onto trigon basin (not observed in *M. sp. cf. M. minutus*); (4) lingual part of anterior cingulum remains broader (usually narrows mark-

TABLE 4
Measurements and Ratios of Upper and Lower Teeth of *Microparamys tricus*
from Ventura and San Diego Counties, California

Specimen No.		Locality	A-P	W	$\frac{A-P}{W}$			
DP ⁴	UCMP 101916	V-72088	1.372	1.438	0.954			
P ⁴	LACM(CIT) 2150	LACM(CIT) 150-E	1.545	1.915	0.807			
M ¹	LACM(CIT) 2150	LACM(CIT) 150-E	1.780	2.015	0.883			
	UCMP 102003	V-72088	1.646	1.872	0.879			
	UCMP 110359	V-72088	1.575	1.833	0.859			
M ²	LACM(CIT) 2150	LACM(CIT) 150-E	1.765	2.122	0.832			
	UCMP 101981	V-72088	1.592	1.758	0.906			
	UCMP 106683	V-72088	1.642	1.898	0.865			
M ³	UCMP 104129	V-72088	1.322	1.383	0.956			
						$\frac{A-P}{W-TRI}$	$\frac{A-P}{W-TAL}$	$\frac{W-TRI}{W-TAL}$
				W-TRI	W-TAL			
DP ₄	UCMP 106614	V-72088	1.420	0.880	1.227	1.614	1.157	0.689
P ₄	LACM(CIT) 1122 ^a	LACM(CIT) 150	1.763	1.475	1.653	1.195	1.067	0.892
	UCMP 101953	V-72088	1.471	1.044	1.258	1.409	1.169	0.830
M ₁	LACM(CIT) 1122 ^a	LACM(CIT) 150	1.765	1.728	1.847	1.021	0.956	0.936
	UCMP 99356	V-72088	1.590	1.489	1.662	1.068	0.957	0.896
	UCMP 106499	V-72088		1.487				
M ₂	LACM(CIT) 1122 ^a	LACM(CIT) 150	1.835	1.997	1.973	0.919	0.930	1.012
M ₃	LACM(CIT) 1122 ^a	LACM(CIT) 150	2.107	1.938	1.694	1.087	1.244	1.144

^aHolotype.

edly lingual to paraconal region in *M. sp. cf. M. minutus*); and (5) ridge from apex of paracone runs more directly lingual (angles more anterior in *M. sp. cf. M. minutus*).

P⁴ as in *Microparamys sp. cf. M. minutus* except: (1) connecting ridge well developed between apex of paraconule and rim of anterior cingulum (usually absent in *M. sp. cf. M. minutus*, but weakly developed when present); (2) metaconule strongly bulbous (weakly or multiply developed in *M. sp. cf. M. minutus*); (3) mesostyle present, centrally placed between paracone and metacone, and with short but distinct ridge running lingual toward trigon basin (usually absent or minuscule in *M. sp. cf. M. minutus* and lacking in projecting ridges); and (4) distinct ridge (analogous to postparaconular wing) runs posterolabial toward mesostyle from apex of paraconule (absent in *M. sp. cf. M. minutus*).

M¹⁻² (figs. 12, 13) as in *Microparamys sp. cf. M. minutus* except: (1) Stronger development of labially directed ridge from apex of protocone onto trigon basin and lingually directed ridge from apex of mesostyle toward trigon basin (commonly present, but much weaker in *M. minutus*); (2) short but consistently developed labially directed spur from anterior part of base of hypocone toward metaconular area (present in only a small percentage of specimens of *M. sp. cf. M. minutus*); (3) tendency toward weakening of ridge between metaconular and protoconal apices (usually well developed in *M. sp. cf. M. minutus*); and (4) tendency toward doubling or multiplication of metaconules (metaconules usually present in *M. sp. cf. M. minutus*, but when present are almost always single and very weak).

M³ (fig. 14) as in *Microparamys sp. cf. M. minutus* except: (1) Loss of connection of metaconular region with postprotocrista (continuous in *M. sp. cf. M. minutus*); and (2) direct connection by ridges of hypoconal with metaconular area (seen as an occasional variant in *M. sp. cf. M. minutus*).

DP₄ (fig. 15) as in *Microparamys sp. cf. M. minutus* except: (1) Anteroconid doubled (single if present in *M. sp. cf. M. minutus*) and set more labially (transversely centrally placed in *M. sp. cf. M. minutus*); (2) postprotocristid slightly sharper in elevation (usually not a distinct crest in *M. sp. cf. M. minutus*) and extends continuously from apex of protoconid to apex of metaconid (usu-

ally runs only between bases of cusps in *M. sp. cf. M. minutus*); (3) distinct hypolophid extends labial from apex of entoconid nearly halfway across talonid basin (not seen in *M. sp. cf. M. minutus*); and (4) weak but distinct ridge runs anterior from apex of protoconid to connect with labial part of anteroconid (not observed in *M. sp. cf. M. minutus*).

P₄ as in *Microparamys sp. cf. M. minutus* except for lacking protoconid (usually present in *M. sp. cf. M. minutus*). M₁₋₃ as in *M. sp. cf. M. minutus* except (fig. 16) that hypolophid (strong and obvious) extends from entoconid apex onto basin of talonid (usually absent or represented as a mere hint in *M. sp. cf. M. minutus*).

Discussion. Although numerous differences do exist between *Microparamys sp. cf. M. minutus* and *M. tricus*, they are of a minor nature except for size. The vast majority of the differences observed in *Microparamys tricus* seem to represent advanced conditions over those seen in *M. sp. cf. M. minutus* and I can see no morphological features in the latter that would bar the possibility of ancestry for the former.

FAMILY SCIURAVIDAE MILLER & GIDLEY, 1918

GENUS *SCIURAVUS* MARSH, 1871

Sciuravus powayensis Wilson, 1940b

Figures 17, 18

Holotype. LACM(CIT) 2281, left mandibular fragment with P₄M₁₋₃.

Type Locality. LACM(CIT) 249, one-fourth mi. NE of Mission San Diego de Alcala, Friars Formation, Mission Valley, San Diego, San Diego County, California (Uintan).

Referred Specimens. 13 isolated DP⁴s; two isolated P³s; LACM(CIT) 2282, P³⁻⁴ M¹; 7 isolated P⁴s; UCMP 106286, M¹⁻²; 13 isolated M¹s; LACM(CIT) 2285, M²⁻³; 25 isolated M²s; 13 isolated M³s; 15 isolated DP₄s; LACM(CIT) 2291, 2292, 2295, P₄M₁₋₃; UCMP 96273, 96341, P₄M₁₋₃; LACM(CIT) 2293, 2296, 2297, 2299, P₄M₁₋₂; 7 isolated P₄s; LACM(CIT) 2298, M₂₋₃; 20 isolated M₁s; 29 isolated M₂s; 16 isolated M₃s. Isolated teeth include both LACM(CIT) and UCMP specimens.

Localities. Friars Fm.: LACM(CIT) 249 and 249-S, V-6873, V-6882, V-6889, V-68101, V-68116, V-68118, V-71056, V-71175, V-71183,

V-71186; Mission Valley Fm.: V-71180, V-71209, V-71211, V-72157, V-72158, V-72176, V-72177, V-72179, V-73138.

Distribution of Species. Friars and Mission Valley formations, greater San Diego area, San Diego County, California (Uintan).

Description. Except for a few peculiar variants, the description by Wilson (1940b) of most of the dentition of *Sciuravus powayensis* remains adequate. Deciduous teeth, however, were not represented in his original material and are described in detail below.

Dental measurements of *Sciuravus powayensis* (tables 5, 6) are as follows:

All upper teeth, permanent and deciduous—A-P, As in *Microparamys* spp. above.

ANT-W, Normal to A-P, measuring greatest width from labial base of paracone to lingual base of protocone.

POST-W, Normal to A-P, measuring greatest width from labial base of metacone to lingual base of hypocone (or if not present, to lingual base of protocone).

All lower teeth, permanent and deciduous—

A-P, Parallel to an axis aligned from area of hypoconulid through center of valley between protoconid and metaconid, but measuring from anterior face of tooth in "paraconid" region to posterior-most base of tooth in region of hypoconulid.

W-TRI, As in *Microparamys* spp. above.

W-TAL, As in *Microparamys* spp. above.

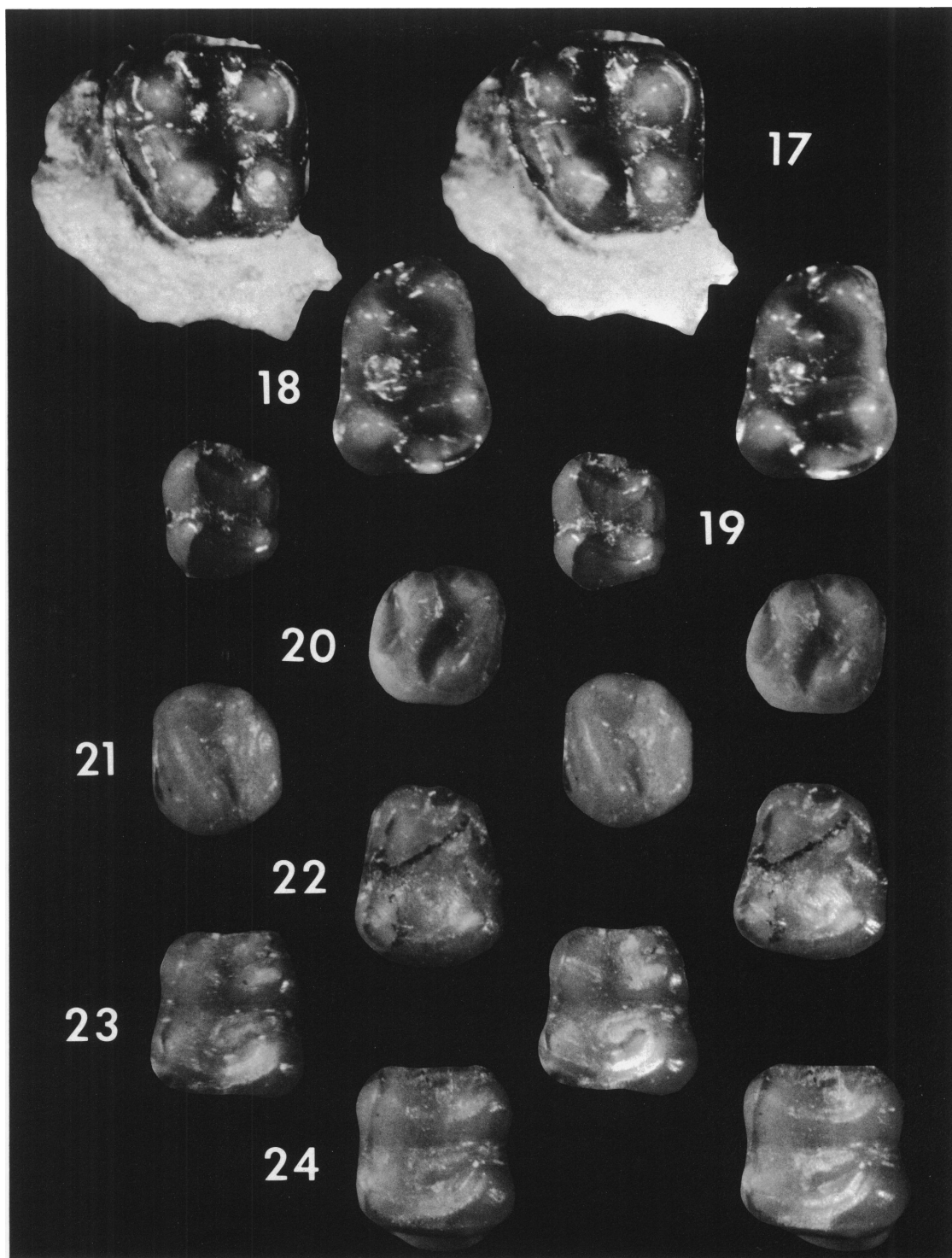
DP⁴. The tooth is fully molariform with a distinct hypocone equally as developed as the protocone (fig. 17). The tooth is proportionally much longer anteroposteriorly than the P⁴ (table 5). The four basic cusps of the crown are nearly equal in height, but the paracone and metacone are usually slightly taller than the lingual cusps. The paracone is generally conical in shape, whereas the metacone is somewhat anteroposteriorly compressed. Both the protocone and the hypocone are rather conical, but a strong ridge runs anterolabially from the apex of each. The anteriormost parts of these ridges are almost always distinctly expanded as a protoconule and metaconule, respectively. The conules are usually distinct from the bases of paracones and metacones, but infrequently there may be weak-ridged connections between them. There are no paralophules or metalophules as such. Also lacking is a mesocone, mures, and an enterostyle.

The anterior cingulum is usually strong as an anteriorly projecting shelf that begins at the anterolabial base of the paracone and terminates at the anterior base of the protocone. There is no anterocone development nor definite parastyle. Almost invariably any anterolabial projection from the protoconule stops well short of the anterior cingulum, but in UCMP 106791 contact is approximated.

The posterior cingulum usually begins about one-third of the way up the posterolabial slope of the metacone, then climbs dorsad and curves linguad to run as a strong structure to terminate at the posterolabial base of the hypocone. On three of 13 specimens, however, the cingulum runs uninterrupted from the posterior side of the tooth around the posterolabial corner of the metacone all the way to the posterolabial base of the paracone. All available specimens have a distinctly raised cingulum-like structure between the bases of the paracone and metacone along the labial border of the crown. Small mesostyles are present on all unworn specimens and they are more commonly doubled than single. The lingual termination of the posterior cingulum at the base of the hypocone shows all stages of intermediacy between the extremes of: (1) Being continuous with the hypoconal mass; and (2) being separated from it by a marked gap.

There is no indication of an appression facet on the anterior face of any available DP⁴, thus suggesting the absence of more anterior deciduous teeth.

The teeth are three-rooted. A proportionally huge lingual root extends dorsad from the combined bases of the protocone and hypocone and its length seems to have been nearly three times the height of the crown. The root extends transversely more than halfway from the lingual toward the labial edge of the crown. Its cross section is highly irregular and it projects dorsolingual relative to the crown surface. The two labial roots are much smaller, probably were significantly shorter, are nearly circular in cross section, and are set directly dorsal to the bases of the paracone and metacone. The metaconal root projects nearly straight dorsad, whereas the paraconal root runs more anteriorly and linguad. Although the unresorbed roots of DP⁴ are nearly of the same size and arrangement as those of the permanent premolar, the root walls of DP⁴ are paper-thin in comparison; the walls of P⁴ are



FIGS. 17, 18. Stereophotographs in occlusal view of left deciduous cheek teeth of *Sciuravus powayensis* Wilson, 1940b from V-71211 (17 \times). 17. UCMP 104471, DP⁴. 18. UCMP 104469, DP₄.

FIGS. 19-21. Stereophotographs in occlusal view of isolated cheek teeth of *Griphomys alecer* Wilson, 1940b from V-72088. 19. UCMP 106732, left M₂ (18 \times). 20. UCMP 99252, right M² (17 \times). 21. UCMP 104141, left ?M³ (21 \times).

FIGS. 22-24. Stereophotographs in occlusal view of isolated right cheek teeth (probably from the same individual) of *Griphomys toltecus*, new species from V-72088 (fig. 22 22 \times , figs. 23, 24 18 \times). 22. UCMP 104088, P₄. 23. UCMP 104083, M₁. 24. UCMP 102009, holotype, M₂.

TABLE 5
Standard Statistics for Upper Teeth of *Sciuravus powayensis* from the
Greater San Diego Area, California

		N	O.R.	\bar{X}	$SE_{\bar{X}}$	S.D.	V	R
A-P	P ³	3	0.852-0.905	0.871				
	DP ⁴	13	1.436-1.845	1.629	0.033	0.119	7.3	
	P ⁴	8	1.408-1.633	1.532	0.028	0.079	5.2	
	M ¹	16	1.616-2.210	1.940	0.043	0.173	8.9	
	M ²	27	1.391-2.187	1.952	0.034	0.174	8.9	
	M ³	14	1.585-2.521	1.872	0.058	0.218	11.6	
W	P ³	3	0.840-0.907	0.876				
	P ⁴	8	1.685-1.936	1.810	0.028	0.080	4.4	
	M ³	12	1.578-2.063	1.891	0.049	0.171	9.0	
ANT-W	DP ⁴	12	1.396-1.709	1.579	0.031	0.107	6.8	
	M ¹	13	1.662-2.223	1.965	0.042	0.150	7.6	
	M ²	25	1.866-2.360	2.089	0.032	0.158	7.6	
POST-W	DP ⁴	12	1.430-1.753	1.601	0.028	0.098	6.1	
	M ¹	14	1.462-2.318	1.971	0.054	0.202	10.2	
	M ²	27	1.683-2.234	1.982	0.027	0.139	7.0	
A-P/W	P ³	3	0.967-1.020	0.995				
	P ⁴	8	0.797-0.887	0.846	0.011	0.031	3.7	0.732
	M ³	12	0.929-1.145	0.992	0.017	0.060	6.0	0.746
A-P/ANT-W	DP ⁴	12	0.977-1.101	1.030	0.011	0.039	3.8	0.901
	M ¹	13	0.924-1.085	0.989	0.013	0.047	4.8	0.487
	M ²	25	0.868-1.043	0.932	0.015	0.074	7.9	0.759
A-P/POST-W	DP ⁴	12	0.932-1.094	1.016	0.016	0.054	5.3	0.793
	M ¹	14	0.901-1.105	0.988	0.015	0.056	5.7	-0.082
	M ²	27	0.724-1.035	0.985	0.013	0.066	6.7	0.067
ANT-W/POST-W	DP ⁴	12	0.992-1.137	0.987	0.016	0.054	5.4	0.921
	M ¹	13	0.976-1.137	1.001	0.013	0.046	4.6	0.056
	M ²	25	0.983-1.141	1.054	0.009	0.046	4.3	-0.156

remarkably thick with only a small-diameter root canal.

DP₄. The basic structure of DP₄ of *Sciuravus powayensis* is much like that of M₁ in *Simimys simplex* (redescribed by Lillegraven and Wilson, 1975, see text-fig. 2, p. 861) and the terminology used is the same. The metaconid is the tallest of the cusps, usually rather conical, and universally has a well-developed lingual lophid (fig. 18). Metastylids are usually absent (seven of 13 specimens) but two specimens show an elevation on the lingual lophid in the expected location, and four show a small but distinct metastylid; in no case has a labial extension of the metastylid been observed. A protoconid is present on all available specimens, but is much lower than the metaconid and the apex of the protoconid is posterolabial to that of the metaconid. The preprotocristid

usually curves anterolingual from the apex of the protoconid to end at the anterolabial base of the metaconid. Only three specimens show even a weak development of an anteroconid. The postprotocristid curves posterolingual from the protoconid apex then turns directly lingual. It is free-ending in all available specimens but points variously toward the wall of the metaconid, the lingual lophid, or the entoconid. A small mesoconid is always present, but labial and lingual mesolophids are lacking and anterior and posterior ectolophids are only weakly developed if present at all. A tiny ectostylid is present on seven of 13 available specimens.

The entoconid is the second highest of the cusps, is anteroposteriorly compressed, and has a strong hypolophulid that runs from its apex to the base of the hypoconid. Two of 15 specimens

show a distinct cuspule-like expansion and elevation of the lingual extreme of the hypolophulid immediately adjacent to the apex of the entoconid. The labial extreme of the hypolophulid usually joins with a short weak ridge running linguad from the apex of the hypoconid.

The hypoconid is conical to slightly compressed anteroposteriorly. The posterior cingulum begins at its posterolingual base and runs in a convex-posterior path to the posterior base of the entoconid. A distinctly enlarged hypoconulid is present on all available specimens and is set equidistantly between the labial and lingual sides of the tooth.

DP₄ is double-rooted. The anterior root is anteroposteriorly elongated in cross section and usually projects somewhat anteriorly toward its ventral tip. The posterior root is transversely nearly as wide as the crown of its talonid, is anteroposteriorly compressed, and it curves slightly posterior toward the ventral tip. Both roots are roughly the same length at slightly more than twice the height of the crown. As with the DP₄, the root walls of DP₄ are remarkably thin, quite in contrast to the thick-walled roots of P₄ with their constricted root canals.

Discussion. Specimen LACM(CIT) 2293 (see Wilson, 1940b, p. 1, fig. 2) is a mandible of *Sciuravus powayensis* with M₁₋₂ and a P₄ that was in the early stages of eruption. Significant wear had already occurred on the molars, especially M₁, despite the fact that the permanent premolar was just starting to come in. This suggests that the DP₄ in *S. powayensis* probably persists throughout much of the young life of the animals. This suggestion is reinforced by the numerical distribution of teeth recovered in the present study; identifiable DP₄s are found in equal abundances (table 6) with P₄s and DP₄s outnumbering P₄s in the collection by a margin of 13 to 8 (table 5). Thus with respect to the "permanence" of deciduous premolars, *S. powayensis* is probably similar to *Microparamys*, and may further strengthen the suggestion of commonality of origin of the two genera (see, for example, Dawson, 1968, p. 340).

Features of the deciduous premolars of *Sciuravus powayensis* are virtually indistinguishable morphologically and morphometrically from DP₄s of *S. eucristadens* (see Dawson,

1968, pp. 344-347) from Bridgerian sediments of northeastern Utah. Deciduous teeth of *S. powayensis* were not available to Wilson (1940b) when he described the species, but even with the material at hand he recognized the similarities with *S. eucristadens*. The morphology of DP₄ of *S. powayensis* as described in the present paper further supports the concept of close phylogenetic relationship between the two species.

During the process of numerical data reduction for the available teeth of *Sciuravus powayensis*, I performed computer-generated bivariate plots of all morphometric data for each tooth within the dental series, keeping track of locality and formational occurrences. All plots of direct measurements were distinctly bimodal with larger teeth generally from the Friars Formation and smaller teeth generally from the Mission Valley Formation. These results were especially clear in the lower molar series as lower teeth are almost always less variable morphometrically than upper teeth. It is likely that in reality two distinct species or "population swarms" are represented within the samples here lumped as "*Sciuravus powayensis*." They are indistinguishable morphologically, however, and considerable statistical overlap occurs in some localities. Isolated teeth with measurements within the range of overlap between the likely two species are at present impossible to identify in one or the other of the two groups.

Interestingly, the bivariate plots of the width measurements for each molar (e.g., W-TRI vs. W-TAL of M₂) show no change in slope in the region expected where teeth referable to one of the groups stop and teeth referable to the other group begin. That is, the slope is straight and unbroken with generally Friars Formation teeth in the upper (larger) one-half and generally Mission Valley teeth in the lower (smaller) half. The coefficient of correlation, for example, of W-TRI vs. W-TAL for M₂s of both groups lumped exceeds 0.93 and the coefficient of variation of that comparison is less than 3. Thus molars of the two groups show no recognizable width-proportional differences from one another but rather are simply of different size. Because of these problems in identification, I see no value in naming a new species for the Mission Valley Formation specimens. It seems preferable, until

TABLE 6
Standard Statistics for Lower Teeth of *Sciuravus powayensis* from the
Greater San Diego Area, California

		N	O. R.	\bar{X}	$SE\bar{X}$	S. D.	V	R
A-P	DP ₄	15	1.676-1.957	1.774	0.020	0.076	4.3	—
	P ₄	16	1.497-1.745	1.628	0.018	0.070	4.3	—
	M ₁	31	1.858-2.205	2.033	0.019	0.104	5.1	—
	M ₂	41	1.855-2.301	2.108	0.020	0.130	6.2	—
	M ₃	23	1.848-2.562	2.226	0.045	0.216	9.7	—
W-TRI	DP ₄	13	0.979-1.228	1.069	0.021	0.075	7.0	—
	P ₄	16	1.075-1.323	1.219	0.021	0.085	6.8	—
	M ₁	30	1.469-1.846	1.667	0.016	0.089	5.3	—
	M ₂	41	1.548-2.143	1.925	0.022	0.141	7.3	—
	M ₃	23	1.576-2.049	1.827	0.030	0.143	7.8	—
W-TAL	DP ₄	13	1.196-1.485	1.322	0.028	0.100	7.6	—
	P ₄	16	1.329-1.620	1.471	0.024	0.095	6.5	—
	M ₁	30	1.710-2.047	1.838	0.015	0.081	4.4	—
	M ₂	41	1.633-2.247	1.999	0.022	0.141	7.0	—
	M ₃	23	1.408-1.951	1.677	0.026	0.124	7.4	—
A-P/W-TRI	DP ₄	13	1.545-1.795	1.667	0.020	0.073	4.4	0.798
	P ₄	16	1.225-1.472	1.339	0.018	0.074	5.5	0.616
	M ₁	30	1.117-1.380	1.221	0.012	0.063	5.2	0.665
	M ₂	41	0.934-1.251	1.097	0.009	0.059	5.4	0.782
	M ₃	23	1.104-1.355	1.216	0.013	0.063	5.2	0.558
A-P/W-TAL	DP ₄	13	1.245-1.489	1.348	0.019	0.067	5.0	0.770
	P ₄	16	0.996-1.209	1.110	0.014	0.055	5.0	0.629
	M ₁	30	1.007-1.197	1.107	0.010	0.054	4.9	0.715
	M ₂	41	0.899-1.186	1.056	0.008	0.053	5.0	0.770
	M ₃	23	1.185-1.421	1.327	0.015	0.073	5.5	0.713
W-TRI/W-TAL	DP ₄	13	0.757-0.856	0.809	0.009	0.033	4.1	0.837
	P ₄	16	0.730-0.884	0.830	0.010	0.040	4.8	0.745
	M ₁	30	0.839-0.974	0.907	0.006	0.033	3.6	0.916
	M ₂	41	0.891-1.009	0.963	0.004	0.025	2.6	0.924
	M ₃	23	1.005-1.266	1.093	0.013	0.063	5.8	0.878

more and better material becomes available, to simply realize that "*Sciuravus powayensis*," as used in this paper, is probably a complex species.

Lindsay (1968) suggested the likelihood of a phylogenetic lineage approximating *Sciuravus powayensis* to *Namatomys fantasia* to *Simimys* spp. in which P₄ (and presumably by implication, P₄¹) in the primitive forms represent the homologue of teeth called "M₁" (and presumably "M₁¹") in the advanced kinds. Associated with this change, according to Lindsay, is the loss of M₃ (and presumably M₃¹) in the end members (i.e., *Simimys*). We now know, however, that all three of these genera coexisted contemporaneously and are all represented within the Mission Valley Formation in the greater San Diego

area. Specimens closely similar to or conspecific with "*Namatomys fantasia*" are currently under study by John J. Chiment of San Diego State University. The coexistence of the three kinds in early Uintan sediments makes the phylogenetic lineage suggested by Lindsay seem unlikely.

The morphological similarity between P₄⁴ of *Sciuravus powayensis* and M₁¹ of *Simimys simplex* is, in my opinion, quite low, even when "*Namatomys fantasia*" is interceded. The similarity is in actuality much greater between the DP₄⁴ of *S. powayensis* and M₁¹ of *S. simplex* (see Lillegraven and Wilson, 1975, pp. 862-863). Thus, following Lindsay's reasoning, it would be more reasonable to suggest that the "M₁¹" of *Simimys* is the homologue of DP₄⁴ in *S. powayen-*

sis. Even this, however, I consider most unlikely. The similarities between DP_4^4 of *S. powayensis* and M_1^1 of *Simimys* are real (although not overwhelming when examined in detail), but I believe them much more likely to be the result of a common ancestry by way of a primitive sciuravid stock and the shifting of genetically based "morphogenetic fields" (see Butler, 1967) of character complexes from one tooth in the dental series to another through geologic time. Testing of this interpretation, however, must await more intensive study of Bridgerian or late Wasatchian rodent assemblages.

FAMILY GEOMYIDAE(?) GILL, 1872

GENUS *GRIPHOMYS* WILSON, 1940b

Griphomys alecer Wilson, 1940b

Figures 19-21

Holotype. LACM(CIT) 2522, right mandibular fragment with P_4M_{1-2} .

Type Locality. LACM(CIT) 207, Tapo Ranch, Uintan part of Sespe Formation, Ventura County, California.

Referred Specimens from San Diego County. All isolated teeth. M^2 s, 99252, 101858, 110054; $?M^3$, 104141; M_2^s , 104404, 106732 (all UCMP specimens).

Locality in San Diego County. UCMP V-72088, ?Santiago Formation, Camp San Onofre, Camp Pendleton Marine Corps Base.

Distribution of Genus. Sespe and ?Santiago formations (Uintan), California and possibly Colter Formation (Chadronian), Wyoming.

Distribution of Species. Sespe and ?Santiago formations (Uintan), California.

Description. All measurements for the genus (tables 7, 8) were taken as defined above for *Sciuravus powayensis*.

M_2 . The two new M_2^s available from V-72088 (fig. 19) are virtually unworn in contrast to the three originally described by Wilson (1940b). Otherwise, they are indistinguishable from the type. The two main concave-anterior transverse lophids have crests that are unbroken even in the unworn state although they are lower in their middles than at their ends. Short sharp crests project posteriad from the apex of the metaconid and anteriad from the apex of the entoconid.

The crest from the metaconid is roughly twice the length of the one from the entoconid. The ends of the two crests terminate sharply without touching each other, leaving a gap in the lingual wall of the tooth. Thus the transverse valley across the tooth between the two main lophids is complete. A vestigial mesoconid is present between the two lophids at the transverse center of the teeth and is slightly more obvious than in the type material; in UCMP 104404 a weak posterior ectolophid runs from the mesoconid straight posteriad to the crest of the posterior lophid near its transverse center. A minuscule ectostylid is present on UCMP 104404. Not the slightest hint of a posterior cingulum is seen on the back wall of the posterior lophid, although the enamel there is slightly crenulated. The anterior cingulum is well developed as a rimmed level shelf beginning at the anterior base of the metaconid and terminating at the anterior base of the protoconid.

The roots are not preserved.

M^2 . LACM(CIT) 2526 (see Wilson, 1940b, pl. 2, fig. 5) is probably an M^1 as judged by its rather square shape seen in occlusal view as allowed by a strong metaconal area; it also agrees well in shape with what is left of the M^1 in LACM(CIT) 2525 (see Wilson, 1940b, pl. 2, fig. 4). The three teeth here identified as M^2 s, on the other hand, have a more reduced metacone, giving the posterolabial corner of the teeth a more rounded shape in occlusal view (fig. 20). The effect is that teeth of this type here identified as M^2 s give the shape appearance typical of M^3 s of less specialized rodents. Well-developed appression facets on the posterior faces of the teeth, however, show that the teeth are not terminal in the dental series.

Wilson's (1940b, p. 94) description of the upper molars holds well for the newly available M^2 s. One minor variation is seen in UCMP 110054 in which a low posterior protocrista is present extending from the apex of the protocone labiad to terminate in the center of the trigon basin, thus mimicking the appearance of the posterior main loph and its continuing posterior cingulum.

The roots are well developed with distinct paraconal and metaconal roots and a united protocone-hypocone root. The labial roots are circular in cross section, only slightly shorter

TABLE 7
Measurements and Ratios of Upper and Lower Teeth of *Griphomys alecer* from
Ventura County and San Diego County, California

	Specimen No.	Locality	A-P	ANT-W	POST-W	A-P	A-P	ANT-W
						ANT-W	POST-W	POST-W
P ⁴	LACM(CIT) 2525	LACM(CIT) 150	1.218	1.205	1.163	1.011	1.047	1.036
M ¹	LACM(CIT) 2525	LACM(CIT) 150	1.130(est.)	—	—	—	—	—
	LACM(CIT) 2526	LACM(CIT) 150	1.242	1.255	1.299	0.990	0.956	0.966
M ²	UCMP 99252	V-72088	1.216	1.288	1.212	0.944	1.003	1.063
	UCMP 101858	V-72088	1.108	1.263	1.206	0.877	0.919	1.047
	UCMP 110054	V-72088	1.220	1.422	1.281	0.858	0.952	1.110
M ³	UCMP 104141	V-72088	1.013	1.168	1.037	0.867	0.977	1.126
						A-P	A-P	W-TRI
						W-TRI	W-TAL	W-TAL
P ₄	LACM(CIT) 2522 ^a	LACM(CIT) 207	1.100	0.787	0.979	1.398	1.124	0.804
	LACM(CIT) 2524	LACM(CIT) 150	1.034	0.711	0.905	1.454	1.143	0.786
M ₁	LACM(CIT) 2522 ^a	LACM(CIT) 207	1.192	1.037	1.191	1.149	1.001	0.871
M ₂	LACM(CIT) 2522 ^a	LACM(CIT) 207	1.224	1.152	1.186	1.063	1.032	0.971
	LACM(CIT) 2523	LACM(CIT) 202	1.255	1.251	1.227	1.003	1.023	1.020
	LACM(CIT) 2524	LACM(CIT) 150	1.219	1.125	1.132	1.084	1.077	0.852
	UCMP 104404	V-72088	1.187	1.096	1.126	1.083	1.054	0.973
	UCMP 106732	V-72088	1.184	1.115	1.077	1.062	1.099	1.035

^aHolotype.

than the proto-hypoconal root, and project straight dorsad from the crown. The proto-hypoconal root is nearly twice the length of the height of the crown, anteroposteriorly underlies all but the posterior cingulum of the crown, and is markedly compressed transversely.

M³. The tooth here tentatively identified as M³ (fig. 21) is like the M² in basic design, but smaller, has a still smaller metaconal area, a reduced hypoconal area, and no observable appression facet on its posterior face. A small but distinct mesocone is placed between the two main lophs at the transverse center of the tooth.

The roots are not preserved.

Griphomys toltecus, new species

Figures 22-24

Etymology. "Toltec," an Aztec people, in honor of the San Diego State University "Aztecs."

Holotype. UCMP 102009, isolated right M₂ (see qualification on nature of type in "Comments on Holotype" section below).

Type and Only Known Locality. UCMP V-72088, Camp San Onofre, Camp Pendleton Marine Corps Base, northernmost San Diego County, California (Uintan).

Referred Specimens. All isolated teeth. P₄, UCMP 104088; M₁, UCMP 104083; M₂, UCMP 110127.

Distribution of Species. ?Santiago Formation (Uintan), California.

Diagnosis. Teeth significantly larger than *Griphomys alecer*; basically as in *G. alecer* except lower molars have: (1) The lingual end of transverse valley blocked by wall and metalophid; (2) a strong mesoconid-labial mesolophid ridge in transverse valley; and (3) preprotocristid retained.

Comments on Holotype. Although the specimen chosen for the holotype of the new species is an isolated M₂, two other isolated teeth clearly of the same species were collected from the same bed on the same day under the same field number (JAL 4099). The other two teeth were P₄ (UCMP 104088) and M₁ (UCMP 104083), all from the right side of the jaw. The relative sizes

of the teeth, the degrees of wear, and the colors of preservation observed are exactly those expected if all three teeth had been from the same individual. Furthermore, out of many man-days of collecting from that particular locality and out of literally thousands of other identifiable specimens, only one other tooth referable to the species was recovered. Thus it seems nearly without question that UCMP 104088 and 104083 should be considered as part of the holotype of this extremely rare new species.

Description. P_4 . Other than its larger size, differences between the P_4 of *Griphomys toltecus* (fig. 22) and the smaller *G. alecer* are minor, being restricted to: (1) The presence of a small but distinct anteroconid (rather than a short and low anterior cingulum in *G. alecer*); and (2) the likely presence of a low metastylid in the unworn state (absent in available specimens of *G. alecer*). There also seems to be some complication on the floor of the talonid (i.e., perhaps a mesoconid and radiating spurs) of the P_4 of *G. toltecus* not seen in *G. alecer*, but the extent of wear is such that details cannot be clearly seen. Otherwise, all details of P_4 between the two species seem to be identical, down to the presence of a tiny ectostylid on the labial edge of the tooth between the bases of the protoconid and hypoconid.

M_{1-2} . M_{1-2} (figs. 23, 24) on the other hand, show some significant differences from homologous teeth in *Griphomys alecer*. Most striking is the presence in *G. toltecus* of a strong transverse ridge in the median valley between the two main lophids that begins just lingual to the transverse center of the tooth and runs labiad, generally decreasing in width and height as it goes, to

nearly the labial edge of the tooth. I interpret this structure as representing the combination of a vestigial mesoconid (at the lingual end of the ridge) with a labial mesolophid (see Lillegraven and Wilson, 1975, text-fig. 2, p. 861) extending labiad from it. There is only the hint of a posterior ectolophid from the probable area of the mesoconid in the form of a posteriorly expanded bump. A second difference is that the antero-posteriorly running ridges on the lingual side of the teeth between the metaconid and entoconid are connected, thus blocking the lingual exit of the transverse valley between the two main lophids. There is even the hint of a metastylid in the area of junction of the two ridges in all three available lower molars of *G. toltecus*.

A third major difference is seen in the area of the labial end of the anterior cingulum and the anterior part of the protoconid. A ridge, here interpreted as a nearly vestigial preprotocristid, connects the protoconid and anterior cingulum well lingual to the labial terminus of the cingulum. Such a connection is not seen in available specimens of *G. alecer*. Finally, the construction of the metalophid in *G. toltecus* seems to be not quite complete in that elements of the hypo- lophulid, posterior cristid of the hypoconid, and posterior cingulum appear to be involved in advanced stages of a process of fusion.

Discussion. The marked size and morphological differences between specimens referable to *Griphomys alecer* and *G. toltecus* leave little doubt as to their distinctness at the species level. Except for its larger size, *G. toltecus* seems to retain the larger number of more primitive characters. For example, assuming that the enamel and wear patterns of the posterior part of

TABLE 8
Measurements and Ratios of Lower Teeth of *Griphomys toltecus*, New Species
from V-72088, Northernmost San Diego County, California

	Specimen No. ^a	A-P	W-TRI	W-TAL	A-P	A-P	W-TRI
					W-TRI	W-TAL	W-TAL
P_4	UCMP 104088	1.298	0.959	1.151	1.353	1.128	0.833
M_1	UCMP 104083	1.455	1.260	1.418	1.155	1.026	0.889
M_2	UCMP 102009	1.549	1.503	1.521	1.031	1.018	0.988
	UCMP 110127	1.547	1.511	1.535	1.024	1.008	0.984

^aSee section entitled "Comments on holotype" as UCMP 102009, 104083, and 104088 are probably from the same individual.

the lower molars are here correctly interpreted, it seems that the metalophid has been formed by a posterior shift of the hypolophulid (on the labial side of the entoconid) and the posterior cristid of the hypoconid to partly fuse with the posterior cingulum, thus forming a single crest. Such a fusion has been totally completed in all available specimens of *G. alecer*, thus giving no hint as to the mode of formation of the metalophid. A second complex of features seen in *G. toltecus* that probably represents the more primitive state is the complication of the transverse valley floor of the lower molars by the presence of a mesoconid-mesolophid unit and the lack of a lingual exit (plus the presence of a labial metastylid) for the transverse valley. The condition seen in *G. alecer* with two main transverse lophids separated by a complete valley is clearly an advanced condition. The retention of a preprotocristid in the molars of *G. toltecus* also seems a more primitive feature.

The protolophid of *Griphomys* appears to be constructed from the extension, expansion, and fusion of the postprotocristid to the metaconid.

The higher category classification of *Griphomys* remains unaided by the materials discussed in the present paper. A reasonable interpretation still seems to be that proposed by Wilson (1940b, p. 95) in assigning the genus with great uncertainty to the Geomyoidea; there simply is nothing yet available to help refine the assignment.

From the point of view of origins, on the other hand, perhaps a new idea can be added. A large number of teeth close to or directly referable to the species named *Namatomys fantasma* by Lindsay (1968) has been recovered from the Friars and Mission Valley formations of the greater San Diego area and from V-72088 at Camp Pendleton. Lindsay identified teeth from the Hartman Ranch local fauna (Uintan) in the Sespe Formation near Sespe Gorge in Ventura County, California, as a new species of *Namatomys* Black, 1965, a genus originally described from early Oligocene sediments of Montana. The newly acquired material is being studied by John J. Chiment of San Diego State University and will be described by him. We both believe that the specimens are representative of a genus quite distinct from *Namatomys* in the original sense of

N. lloydi Black, 1965. Phylogenetic relationships between the incipiently bilophate molar pattern of "*N. fantasma*" and the fully bilophate pattern characteristic of *Griphomys* are now under study by Chiment. Tentatively, at least, the above-described interpretation of the origin of the transverse lophids in *Griphomys* seems fully consistent with an ancestry from a species near "*N. fantasma*."

The possibility suggested by Sutton and Black (1975) that *Griphomys* also lived in the Western Interior is intriguing in that the genus heretofore had been considered a West Coast Eocene endemic.

FAMILY CYLINDRODONTIDAE MILLER AND GIDLEY, 1918

GENUS *PAEUMYS* PETERSON, 1919

Paeumys sp. near *P. grangeri* Burke, 1935
Figures 25-28

Holotype. *P. grangeri*: AMNH 1869, right mandible with P_4M_{1-3} .

Type Locality. White River, Wagonhound Member, Uinta Formation, Uinta County, Utah.

Referred Specimens. *P.* sp. near *P. grangeri*: DP^4_s , UCMP 106329, 109957; P^4M^1 , UCMP 110231; $?P^4$, UCMP 109732; M^1_s , UCMP 99442, LACM(CIT) 2229; M^2_s , UCMP 110240, LACM(CIT) 2230, 2231; M^x_s , UCMP 96313, 104318; DP_4 , UCMP 96369; P_4s , UCMP 104205, 109763; M_{1-3} , LACM(CIT) 2225, 2226; M_{1-2} , LACM(CIT) 2227; $M_2?$, UCMP 96377.

Localities. *P.* sp. near *P. grangeri*: Friars Fm.: LACM(CIT) 249 and 249-S, V-6873, V-6882, V-68101, V-71175; Mission Valley Fm.: V-6893, V-72157, V-72179, V-73138.

Combined Distribution. *P. grangeri* and *P.* sp. near *P. grangeri*: Uinta Formation, Uinta County, Utah; Friars and Mission Valley formations, greater San Diego area, San Diego County, California (all Uintan).

Description. All measurements for the genus (tables 9, 10) were taken as defined above for *Sciuravus powayensis*.

DP^4 . Premolars, permanent and deciduous, were not present in the samples from San Diego available to Wilson (1940c) thus the newly collected material will be described here. UCMP 109957 (fig. 25) has all the features that one

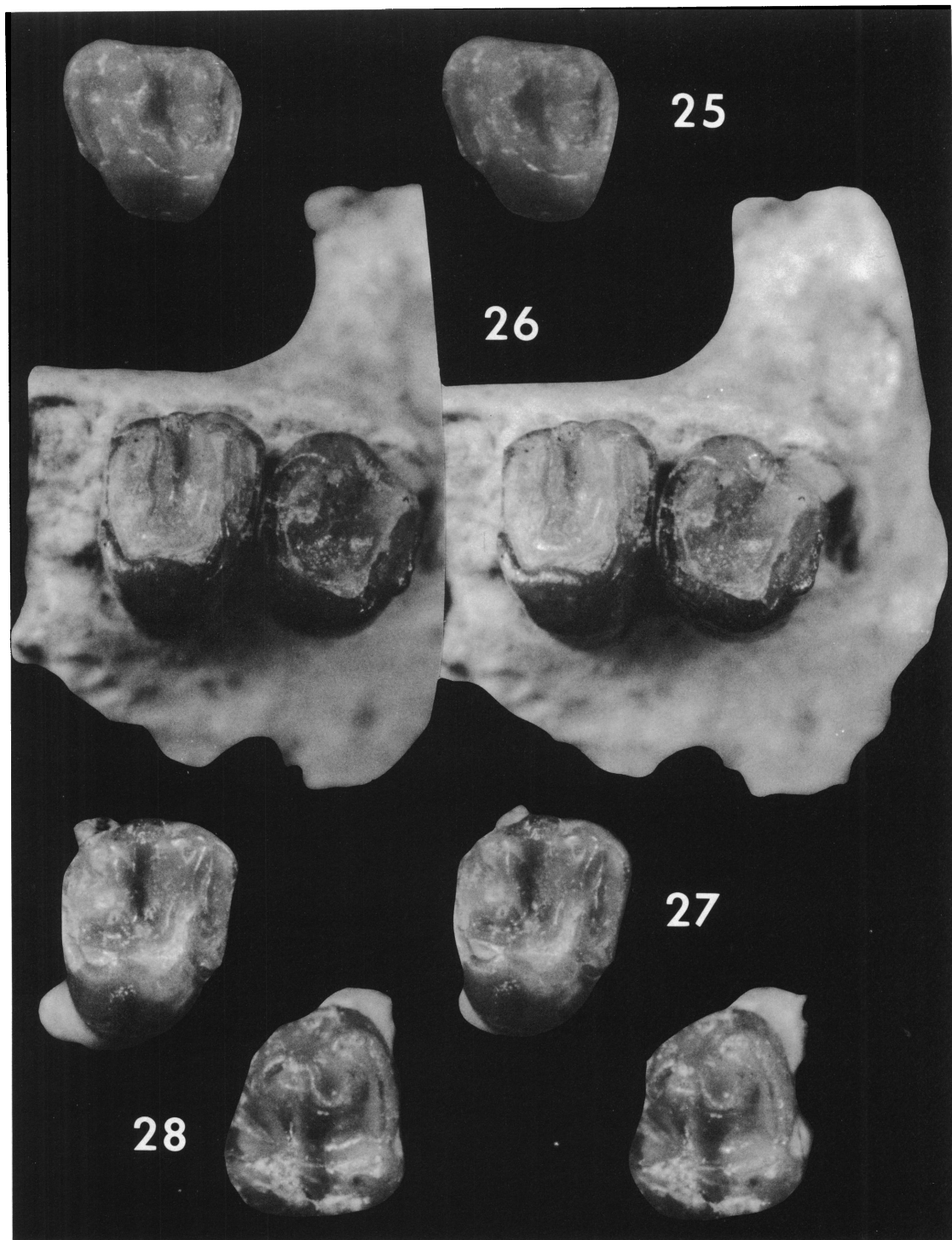
might expect in a DP⁴ of *Pareumys*, and it is quite unlikely that it belongs to another taxon. The tooth crown is constructed delicately of very thin enamel and the roots have been fully resorbed. The labial border is quite straight in occlusal view. An anteroposteriorly broad cingulum begins at the labial base of the paracone, swings in a broad curve anterolingually then turns posterolingually to terminate at the anterior base of the protocone immediately anterior and well dorsal to its apex. The cingulum has a substantially elevated anterior rim. The paracone is the smallest of the trigon cusps as a low cone with a weak paralophule on its lingual side. A rather distinct protoconule is present as an elevation on the preprotocrista and is nearly equal in development with the paracone. The protoconule is by far the most robust of the cusps and is compressed diagonally with a postprotocrista running posterolinguad from its apex to a clearly defined hypocone. The lingual base of the hypo-

cone projects lingual to the base of the protocone and there is only the faintest vertical valley on the lingual side of the tooth to separate the protocone from the hypocone. The posterior cingulum runs unbroken from the apex of the hypocone to the posterolabial base of the metacone. The cingulum is strongly rimmed posteriorly.

The metacone is a tall conical spire, distinctly taller and slightly larger at the base than the paracone. A weak cingulum with the hint of a mesostyle runs along the labial margin of the tooth between the paracone and metacone. A distinct conical metaconule is present that is equal in height with the paracone. Although the bases of the metacone and metaconule are fused, there are no well-defined ridges connecting their apices. The metaconule is surrounded by a deep valley on its other three sides. Thus there is no metaloph as such and the protoloph is only primitively developed.

TABLE 9
Measurements and Ratios of Upper and Lower Teeth of *Pareumys* sp. near *P. grangeri*
from the Greater San Diego Area, California

Specimen No.		A-P	ANT-W	POST-W	$\frac{A-P}{ANT-W}$	$\frac{A-P}{POST-W}$	$\frac{ANT-W}{POST-W}$
DP ⁴	UCMP 106329	1.464	1.656	1.667	0.884	0.878	0.993
	UCMP 109957	1.372	1.362	1.390	1.007	0.987	0.980
P ⁴	UCMP 110230	1.498	1.904	—	0.787	—	—
M ¹	LACM(CIT) 2229	1.036	1.857	1.787	0.558	0.580	1.039
	UCMP 110230	1.430	1.882	1.777	0.760	0.805	1.059
M ²	LACM(CIT) 2230	1.569	1.769	1.683	0.887	0.932	1.051
	LACM(CIT) 2231	1.745	1.895	1.852	0.921	0.942	1.023
	UCMP 110240	1.590	1.995	1.812	0.797	0.877	1.101
			W-TRI	W-TAL	$\frac{A-P}{W-TRI}$	$\frac{A-P}{W-TAL}$	$\frac{W-TRI}{W-TAL}$
DP ₄	UCMP 96369	1.691	0.918	1.117	1.842	1.514	0.822
P ₄	UCMP 104205	1.684	1.172	1.363	1.437	1.236	0.860
	UCMP 109763	1.497	1.178	1.372	1.271	1.091	0.859
M ₁	LACM(CIT) 2225	1.732	1.447	1.663	1.197	1.041	0.870
	LACM(CIT) 2226	1.628	1.480	1.595	1.100	1.021	0.928
	LACM(CIT) 2227	1.645	1.471	1.577	1.118	1.043	0.933
M ₂	LACM(CIT) 2225	1.770	1.527	1.688	1.159	1.049	0.905
	LACM(CIT) 2226	1.788	1.660	1.706	1.077	1.048	0.973
	LACM(CIT) 2227	1.849	1.682	1.733	1.099	1.067	0.971
M ₃	LACM(CIT) 2225	2.152	1.558	1.541	1.381	1.396	1.011
	LACM(CIT) 2226	2.237	1.860	1.835	1.203	1.219	1.014



FIGS. 25-28. Stereophotographs in occlusal view of cheek teeth of *Pareumys* sp. near *P. grangeri* Burke, 1935 (fig. 25 21 \times , figs. 26, 27 17 \times , fig. 28 20 \times). 25. UCMP 109957, left DP⁴ from V-72179. 26. UCMP 110230, right maxillary fragment with P⁴M¹ from V-73138. 27. UCMP 110240, right M² from V-73138. 28. UCMP 104205, left P₄ from V-68101.

Specimen UCMP 106329 is fundamentally similar to the above-described P^4 , but is considerably larger, proportionally wider transversely, and has a more convex labial border in occlusal view. The tooth is quite heavily worn, thus the identification both as to species and as to its deciduous nature is far more in doubt than UCMP 109957.

P^3 . Specimen UCMP 110230 (fig. 26) is a maxillary fragment with P^4M^1 . A minute alveolus for P^3 is present immediately lingual to the anterolabial root of P^4 and a tiny but clear appression facet for P^3 is observed on the anterior face of P^4 at its transverse center. The P^3 could have been little more than the tiniest of pegs. Also, the bone surrounding the alveolus of P^3 is roughened and appears to have been in the process of closing over even though the P^4M^1 of the animal were not severely worn. The probability seems high that the vestigial P^3 was in the process of being lost, at least in that particular individual, in rather early stages of its life.

P^4 . The tooth on UCMP 110230 (fig. 26) is nearly as wide transversely as M^1 and exceeds it slightly in anteroposterior length. The P^4 and upper molars are unilaterally hypsodont with the lingual side of the crown being nearly twice as tall as the labial side. Unfortunately, the anterolabial corner of the crown is missing, but the remnants clearly show that the labial side of the tooth (when seen in occlusal view) was distinctly indented between the convex bases of the paracone and metacone. A minuscule mesostyle was present on the labial margin at the deepest point of the indentation. The labial point of origin of the anterior cingulum is indeterminable, but it is heavily rimmed, anteroposteriorly narrow, and descends posteroventrad as a ridge at its lingual termination to join with the protoloph just anterior to the protoconal apex.

The paracone is largely broken away but seems to have been equal in height with the metacone. The protoloph is complete in running between the apices of the paracone and protocone. A minor protoconular expansion is seen on the protoloph. The protocone is broadly convex lingually and includes the hint of an expansion as a hypocone on the postprotocrista. The posteriorly convex posterior cingulum continues uninterrupted from the hypoconal area to the apex of the metacone at its posterolabial side. The

metacone is a broad low cone with a metaloph projecting linguad and somewhat posteriad from its apex. The metaloph is incomplete lingually, terminating at about two-thirds the distance from the metaconal apex to the hypoconal area. Contact between the lingual end of the metaloph and the posterior cingulum occurs only after heavy wear. The trigon basin is broadly extensive transversely and anteroposteriorly.

The tooth is three-rooted with a proportionally huge proto-hypoconal root and two much smaller labial roots. The roots are roughly twice the length of the height of the crown. The proto-hypoconal root seems to be nearly circular in cross section near the crown and extends transversely nearly two-thirds the distance from the lingual toward the labial edge of the crown. The paraconal root is by far the smallest in cross section and projects anterodorsad from the base of the paracone. The metaconal root is at least twice the diameter of the paraconal root and appears to project straight dorsad.

M^{1-2} . The known upper molars (figs. 26, 27) are similar in basic construction with P^4 except for the following differences. M^{1-2} : (1) are anteroposteriorly shorter in relative and absolute measurements; (2) are wider transversely in the paraconal than metaconal halves; (3) have a markedly more distinct hypocone with a minor indentation between protocone and hypocone visible externally on the lingual wall of enamel; (4) have a transversely straight posterior cingulum that terminates on the posterior side of the apex of the metacone; (5) have a stronger mesostyle; (6) have a less conspicuous or missing ridged connection between the area of the lingual terminus of the anterior cingulum and the crest of the protoloph; (7) have an anteroposteriorly less broad proto-hypoconal root; and (8) have paraconal and metaconal roots equal in diameter that both extend straight dorsad. The labial termination of the anterior cingulum on M^{1-2} is at the anterior base of the paracone. P^4 and M^{1-2} are identical in all other respects and the P^4 is really quite molariform.

It should be emphasized here that the lingual part of the metaloph on P^4M^{1-2} of all known specimens of *Pareumys* sp. near *P. grangeri* is free-ending with no direct connection with or curvature toward the posterior cingulum until advanced stages of wear are reached.

Anterior zygomatic root. A section of the maxilla with the proximal part of the anterior zygomatic root is preserved on UCMP 110230 (fig. 26). The root is strong and its anterior face is nearly vertical but slopes a few degrees posteriad ventrally. A strong bump of bone is present immediately lateral to the alveolus of P^3 on the most proximal part of the anteroventral surface of the root. The "bump" is anteroposteriorly compressed, convex anteriorly, slightly concave posteriorly, and presumably strengthened the origin of the lateral masseter muscle. The beginning of a laterally running ridge on the anteroventral border of the zygomatic arch is separated by a gap from the lateral terminus of the proximal bump. The ventral surface of the zygomatic plate slopes posteroventrad at an angle of about 40 degrees from the horizontal (as defined by the alveolar margin). Only the ventral floor of the infraorbital canal is present, but its greatest lateral diameter seems to have been about four-fifths of the greatest transverse measurement of the P^4 .

Although there probably does not exist enough of the area to be absolutely certain, the existing zygomatic structure suggests a "protrogomorph" or "primitive sciurormorph" masseteric arrangement.

DP_4 . Specimen UCMP 96369 is a peculiar tooth with extremely thin enamel, resorbed roots, and the cusp and crest arrangement basically similar to lower molars of *Pareumys*; it is here identified as DP_4 of *P. sp.* near *P. grangeri*. The metaconid is the tallest and most anterior cusp of the tooth. It has a pointed vertical anterior face and a gently-sloping posterior face. A low ridge runs along the lingual edge of the tooth from the apex of the metaconid to the base of the entoconid. There is no indication of the existence of a metastylid. The protoconid is weak with its apex set well posterolabial to the apex of the metaconid. The specimen is worn in the area of the protoconid but it appears that in unworn specimens a short weak ridge (anterior cingulum?) connects the anterolabial base of the metaconid with the anterior base of the protoconid. A short and weak postprotocristid runs from the lingual base of the protoconid to the posterolabial base of the metaconid. Thus a minuscule trigonid basin (a mere pit) is enclosed

between the two ridges. The basin is quickly obliterated by wear and a posterolabially aligned common wear surface is formed composed of the protoconid plus metaconid.

The talonid of DP_4 is grotesquely exaggerated, making up roughly three-fourths of the total tooth length. The entoconid is set only a short distance posterior to the anteroposterior midpoint of the tooth and sends a strong ridge (?hypolophulid I of Wood and Wilson, 1936) labiad and slightly anteriad to connect with the equally strong ectolophid. The ectolophid begins at the posterior base of the protoconid, runs posterolingual to the point of contact with the ridge of the entoconid, then turns sharply posterolabial to terminate at the hypoconid. There is no mesoconid or ectostylid. The hypoconid is diagonally compressed with a spur projecting anterolabial from the apex of the cusp and a ridge (posterior cingulum) projecting posterolingual to a markedly elevated hypoconulid. The hypoconulid is the tallest cusp of the talonid and nearly reaches the height of the metaconid. A short ridge extends lingual and slightly anteriad from the apex of the hypoconulid to terminate at the lingual margin of the tooth. A deep gap separates the lingual terminus of the posterior cingulum from the entoconid.

Thus DP_4 is basically an overgrown talonid with a great shallow basin divided transversely near its midpoint by the labially extending ridge of the entoconid.

P_4 . Two little-worn isolated P_4 s (fig. 28) referable to *Pareumys sp.* near *P. grangeri* give considerably more morphological information than the heavily worn specimen (LACM [CIT] 2209) available to Wilson (1940c). The protoconid and metaconid are nearly the same in diameter and relative development, but the metaconid is slightly taller and is set more anteriorly. There is no anteroconid nor anterior cingulum, but a strong metalophulid runs posterolabial from the apex of the metaconid to the anterolingual base of the protoconid. An equally strong postprotocristid runs unbroken from the apex of the protoconid to the apex of the metaconid in a markedly convex-posterior path. Thus an enamel lake is isolated between the protoconid and metaconid bounded anteriorly by the metalophulid and posteriorly by the postprotocristid.

The enamel lake is obliterated in rather early stages of wear (as in UCMP 109763) to form a diagonally aligned and continuous protolophid. A strong lingual lophid begins at the apex of the metaconid and runs straight posteriad to terminate with a free end just anterior to the base of the entoconid; there is no metastylid as such, but the posterior half of the lingual lophid is slightly elevated.

The ectolophid is the strongest crest of the tooth and runs without interruption from the apex of the protoconid to the apex of the hypoconid in a concave labially path. There is no hint of a mesoconid or ectostylid. The entoconid is anteroposteriorly compressed with a hypolophulid connected to the ectostylid immediately anterior to the junction with the hypoconid. The hypolophulid is apparently quite variable in its development. It is a strong crest in UCMP 104205 in which it runs to the crest of the ectolophid but in UCMP 109763 it is much weaker running only to the base of the ectolophid. The structure of the hypoconid and posterior cingulum is as in DP₄ except that the hypoconulid in P₄ is recognizable as only the slightest elevation at the transverse center of the posterior cingulum.

Lower molars. Only one fragment of a ?M₂ was recovered in the present study, thus no new information can be added beyond that discussed by Wilson (1940c).

Discussion. An understanding of West Coast *Pareumys* still remains almost as difficult as when Wilson (1940c) pioneered the study; materials are relatively uncommon, usually are disassociated, and the needed "overlap" of equivalent parts for comparative purposes is rarely present. The newly collected fossils from the greater San Diego area help in that deciduous and permanent premolars could be described for the first time, but add little to the task of placing *P. sp. near P. grangeri* into its proper phylogenetic context. Available specimens do, indeed, have profound similarities with such Bridgerian species as *Mysops boskeyi* Wood, 1973 (from Texas) and a rather close relationship seems clear. In some respects, however, *M. boskeyi* seems more specialized than *P. sp. near P. grangeri*. For example, several specimens of *M. boskeyi* (see Wood, 1973, fig. 3, p. 17) show

incipient or real contact of the lingual end of the metaloph on upper molars with the posterior cingulum; there is no suggestion of such a contact in the San Diego material, although it is seen in *Pareumys* teeth from geologically younger strata (see discussion for *Pareumys sp. below*). Thus a direct lineage of *M. boskeyi* to *P. sp. near P. grangeri* is probably unlikely; the distinctness of the two species, at least, seems clear. Any generic distinction between an advanced species of *Mysops* and a primitive species of *Pareumys* is probably quite arbitrary.

Similarities are also great between *Pareumys sp. near P. grangeri* and such later Uintan forms as *Spurimus* Black, 1971 (from Wyoming), especially *S. scotti* (see, for example, Black, 1971, fig. 51, p. 208). *Spurimus* has been considered as a member of the Ischyromyidae by Black. Species of *Mysops* and *Pareumys*, on the other hand, are usually considered as primitive representatives of the Cylindrodontidae. Similarities between such forms as *P. sp. near P. grangeri* and *S. scotti* probably are the result of retention of primitive features held by the last common ancestor of the two species. Wahlert (1974, pp. 407-408), on the basis of arrangement of cranial foramina, suggested that ischyromyid and cylindrodontid rodents were closely related, and that the familial rank of Ischyromyidae be expanded to hold two subfamilies, the Ischyromyinae and the Cylindrodontinae. Such relationships might explain the perplexing similarities between primitive "cylindrodontids" and younger supposed "ischyromyids" such as *Spurimus*. Wood (1974, fig. 13) presented yet another taxonomic interpretation of the Cylindrodontidae, but did not specifically discuss phylogenetic relationships with other families.

I certainly agree with Wilson's 1940c interpretation of the San Diego material as representing the most primitive species yet known for the genus *Pareumys*. The degree of hypsodonty shown is slight and the lophs are generally less elevated and complete than in later Uintan kinds known from California and Wyoming (see Black, 1970 and 1974). It shows no particular specializations toward *Jaywilsonomys* Ferrusquia-Villafranca and Wood, 1969, a supposed descendant of *Pareumys* from the northeastern Chihuahuan ?early Oligocene.

Pareumys sp.

Figures 29-32

Included Specimens. All isolated teeth: M¹s, 99251, 101865; M²s, 99456, 106739; M³, 102000; M^xs, 101772, 106736; DP₄, 101807; M₃s, 102008, 104040, 104183, 106310, 106747 (all UCMP specimens).

Locality. UCMP V-72088, Camp San Onofre, Camp Pendleton Marine Corps Base, northernmost San Diego County, California (Uintan).

Distribution of Species. Santiago Formation (Uintan), California.

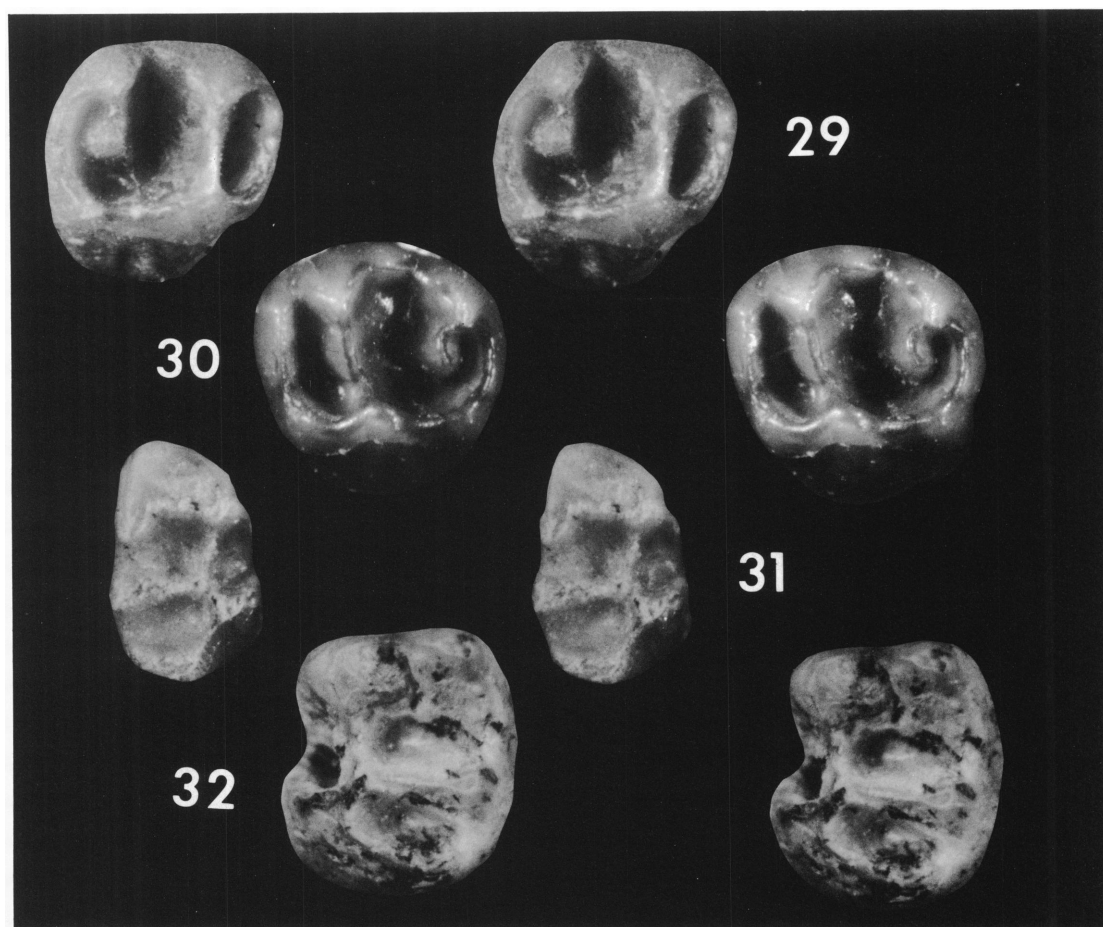
Description. Upper molars. The upper molars of *Pareumys* sp. from V-72088 (fig. 29) are significantly larger than those of the same genus from the greater San Diego area, are slightly more hypsodont, and have a slightly greater degree of separation of the hypocone from the protocone as seen by the vertical groove on the lingual surface of the tooth. The structure of the metaloph is of particular interest. Its lingual termination, although free-ending until advanced stages of wear, is turned sharply posteriad toward the transverse midpoint of the posterior cingulum. That is, the metaloph is nearly perfectly intermediate in structure between *P.* sp. near *P.*

grangeri in which the metaloph terminates pointing straight lingually and *P.* sp. near *P. milleri* (as defined by Wilson, 1940c, p. 100) in which the metaloph terminus turns sharply posteriad and makes a strong fusion with the posterior cingulum.

UCMP 102000 (fig. 30) represents the only known M³ for the genus from the West Coast. It is nearly circular in outline as seen in occlusal view. The anterior cingulum is strong. It begins at the apex of the protocone, runs anterolingual for a short distance, then turns sharply labial to terminate immediately anterior to the base of the paracone. The deep valley between the anterior cingulum and the protoloph is open labially. The paracone has a strong protoloph that runs uninterrupted from its apex to the apex of the protocone. An elevation is present on the protoloph in the expected region for a "protoconule." A low but distinct mesostyle is attached to the posterior base of the paracone. The protocone is the tallest and most massive of the cusps. The posterior cingulum begins at the apex of the protocone, runs posteriad and slightly lingual to the relatively weak hypocone then continues to the apex of the metacone in a strongly convex-posterior arc. A shallow, rounded, vertical trough

TABLE 10
Measurements and Ratios of Upper and Lower Teeth of *Pareumys* sp. from V-72088,
Northernmost San Diego County, California

	Specimen No.	A-P	ANT-W	POST-W	A-P	A-P	ANT-W
					ANT-W	POST-W	POST-W
M ¹	UCMP 99251			2.202			
	UCMP 101865	1.972	2.231	2.239	0.884	0.881	0.996
M ²	UCMP 99456	1.818	1.867	1.824	0.974	0.997	1.024
	UCMP 106739	1.667					
			W	A-P			
				W			
M ³	UCMP 102000	1.972	1.919	1.028			
			W-TRI	W-TAL	A-P	A-P	W-TRI
					W-TRI	W-TAL	W-TAL
DP ₄	UCMP 101807	1.848	1.102	1.202	1.677	1.537	0.917
M ₃	UCMP 102008	2.035	1.808	1.845	1.126	1.103	0.980
	UCMP 104183		1.748				
	UCMP 106310	2.062	1.773	1.566	1.163	1.317	1.132



FIGS. 29-32. Stereophotographs in occlusal view of isolated cheek teeth of *Pareumys* sp. from V-72088 (17 \times). 29. UCMP 99456, right M². 30. UCMP 10200, left M³. 31. UCMP 101807, right DP₄. 32. UCMP 102008, left M₃.

on the lingual surface of the tooth separates the protocone from the hypocone.

The metacone is lower than the paracone but taller than the hypocone. The metaloph begins in an anterolingual direction from the apex of the metacone and makes a short tight anteriorly convex curve to terminate with its free end pointing toward the center of the posterior cingulum. There is no metaconule as such unless the entire metaloph is considered the metaconule. The central trigon basin is deep and its floor is in the shape of the letter J with the hook running around the free end of the metaloph. A short weak crest proceeds anterolabial from the apex

of the metacone to terminate just short of the base of the mesostyle.

As in the more anterior molars, the lingual half of the tooth is far more hypsodont than the labial half.

DP₄. Except for its considerably larger size, DP₄ of *Pareumys* sp. from V-72088 (fig. 31) is identical with that described above for *P. sp.* near *P. grangeri*.

Lower molars. Only terminal molars were recovered from the lower molar series from V-72088 (fig. 32). They are indistinguishable from such specimens as LACM(CIT) 2218 from the Sespe Formation.

Discussion. Identification of the *Pareumys* specimens from V-72088 is presently impossible beyond the generic level. The material is clearly representative of a species distinct from the samples from the greater San Diego area. The Camp Pendleton specimens are significantly larger, slightly more hypsodont, and have more elevated and more completely constructed lophs. Relationships with the various taxa discussed by Wilson (1940c) from the Sespe Formation, however, are less clear.

It is generally understood that an evolutionary trend is seen in the structure of the metaloph within the genus *Pareumys*. The primitive condition as seen, for example, in *P. sp.* near *P. grangeri* from the San Diego area, is with the lingual termination of the metaloph ending free and pointing straight linguad. The presumably most specialized state is seen in *P. sp.* near *P. milleri* from the Pearson Ranch level of the Sespe Formation in which the lingual end of the metaloph turns sharply posteriad to fuse strongly with the posterior cingulum. Assuming that ob-

served intermediate stages of such a transition can be used in determining relative ages of enclosing sediments, the Camp Pendleton *Pareumys* material suggests a geologic age intermediate between the Friars–Mission Valley specimens and the Sespe specimens; the lingual end of the metaloph makes a sharp hook posteriad, but contact is not made with the posterior cingulum until advanced stages of wear occur. The picture becomes less clear, however, when one realizes that even in more primitive species related to *Pareumys* such as *Mysops boskeyi* from supposedly Bridgerian sediments the lingual end of the metaloph has already made contact with the posterior cingulum (see Wood, 1973, fig. 3, p. 17). Thus it seems that the above-described evolutionary trend occurred at least twice at different geologic intervals, and possibly several times in different lineages. If that is true, unquestioning dating of strata on the basis of metaloph development without understanding the lineages themselves could be hazardous, indeed.

SUMMARY AND GENERAL DISCUSSION

A variety of species of small rodents from two stratigraphically and geographically distinct areas within San Diego County, California, are discussed. The areas include the older beds in and immediately around the city of San Diego (Mission Valley and Friars formations) and the younger beds in the northwesternmost corner of the county at Camp Pendleton Marine Corps Base (?Santiago Formation). Two species of *Microparamys*, *Sciuravus powayensis*, and two species each of *Griphomys* and *Pareumys* (see table 11) are discussed. All species recorded from the greater San Diego area have been found both in the Friars and Mission Valley formations and, except perhaps for *S. powayensis*, show no presently recognizable differences between the two formational occurrences. No species and only two of the genera within the present study have been found in common between the sediments of the greater San Diego area and the Camp Pendleton locality (V-72088). In contrast, all genera and possibly three species from V-72088 discussed within the present study have also been

found in the Uintan part of the Sespe Formation from Ventura County, California.

The species of *Microparamys* from the greater San Diego area is identified as *M. sp.* cf. *M. minutus*. Minor differences in size and morphology do exist between the type material of *M. minutus* from “Bridgerian” (roughly late early Eocene) beds of Wyoming and the specimens from San Diego. The exact locality and stratigraphic level of collection of the Wyoming type material are unknown, thus secure identification of the San Diego specimens beyond the present level may never be possible. Other more extensive materials collected from Bridgerian (Powder Wash) sediments of northeastern Utah, however, are virtually indistinguishable morphologically or morphometrically from the San Diego specimens. Dawson (1968) identified the Utah sample as *M. minutus*, although it may not be directly referable to the species represented by the type material. In any case, the Powder Wash and San Diego samples are so similar that a paleontological conspecific status can be assigned

TABLE 11
Summary of Formational Occurrences of Rodent Species Discussed in Detail in Present Paper

	Greater San Diego Area		Camp Pendleton	Ventura Co.
	Friars Fm.	Mission Valley Fm.	?Santiago Fm.	Sespe Fm.
<i>Microparamys</i> sp. cf. <i>M. minutus</i>	+	+	—	—
<i>Microparamys tricus</i>	—	—	+	+
<i>Sciuravus powayensis</i>	+	+	—	—
<i>Griphomys alecer</i>	—	—	+	+
<i>Griphomys toltecus</i> , new species	—	—	+	—
<i>Pareumys</i> sp. near <i>P. grangeri</i>	+	+	—	—
<i>Pareumys</i> sp.	—	—	+	—

to them. The species has dental features generally considered quite primitive for the genus.

Microparamys tricus is found in V-72088 and, as far as available materials allow comparison, is indistinguishable from the type material for the species from the Sespe Formation of Ventura County. The species is larger than *M. sp. cf. M. minutus* from the San Diego area and morphological features are generally more advanced. Morphological differences are minor, however, and with present evidence, an ancestry of *M. tricus* from *M. sp. cf. M. minutus* cannot be ruled out.

"*Microparamys* sp. D" (of Wood, 1962) from the Sespe Formation is a distinct and morphologically advanced species. The establishment of a new name is avoided, however, in hopes that further collecting will increase the hypodigm and thereby allow a more thorough diagnosis.

The high abundance of deciduous premolars relative to permanent teeth in the *Microparamys* samples from San Diego allows the suggestion that, as in many modern sciurids, the milk teeth were retained well into adult life. Other possibilities, however, include high differential mortality of juveniles and/or some peculiarity of the habitat that favored preservation of juveniles.

Species of *Sciuravus* are as yet unknown from the Sespe Formation or V-72088, though they are common in Eocene beds of the greater San Diego area. Distinct bimodality of direct measurements (though not of derived proportional ratios nor any observed morphological feature) of teeth from the Friars vs. Mission Valley formations suggests that "*Sciuravus powayensis*" may

have been a complex species which in reality included two extremely closely related species. Considerable statistical overlap occurs in some localities, however, thus negating the possibility of secure identification of many isolated teeth. No benefit was seen in formally naming a new species of *Sciuravus*.

As in *Microparamys*, an unusually high relative proportion of deciduous premolars was recovered for *Sciuravus*, suggesting a long-term retention of milk teeth during the life of an individual. Such an interpretation is supported in *Sciuravus* by evidence from a jaw. Thus one additional positive comparison is made between the two genera, perhaps further supplementing the argument that they had a close common ancestry. Relationships of *Sciuravus* with *Simimys*, however, seem more remote; I consider the possibility of the ancestry of *Simimys* from something like *Sciuravus powayensis* as suggested by Lindsay (1968) to be highly unlikely. Profound similarities of deciduous premolars between *Sciuravus powayensis* and *S. eucristadens* from Bridgerian sediments of northeastern Utah further support the long-standing idea of a close relationship between the two species.

Species of *Griphomys* have not been found in the greater San Diego area. Specimens indistinguishable from the type material of *G. alecer* of the Sespe Formation, however, have been recovered from V-72088. Larger teeth of a new species, *G. toltecus*, have also been found in V-72088. Specimens of *G. toltecus* are extremely rare and have a suite of characters that most would consider to be more primitive than the

more completely bilophodont *G. alecer*. Abundant specimens yet to be described that represent a species conspecific with or very closely related to *Namatomys fantasma* (*sensu* Lindsay, 1968) from the greater San Diego area suggest incipient bilophodonty and other features allowing the distinct possibility for ancestry to *Griphomys* spp. The systematic relationships of "*Namatomys fantasma*," however, have yet to be established. No further evidence from the present study has come about to suggest the appropriate systematic position of *Griphomys*. Recent finds of specimens possibly referable to *Griphomys* from the Rocky Mountain region suggest that the long-held concept of the genus as representing a West Coast Eocene endemic may be wrong. I agree with Wilson (1940c) in that the specimens of *Pareumys* from the greater San Diego area should be identified as *P. sp.* near *P. grangeri*. The teeth morphologically represent the most primitive yet described for the genus and distinction from advanced species of its Bridgerian presumed ancestor *Mysops* is probably arbitrary. Similarities are also great with later Uintan supposed ischyromyids such as *Spurimus scotti* from Wyoming. Such is interesting because *Pareumys* and *Mysops* are generally considered cylindrodontids. The likelihood seems good, in agreement with information derived from comparisons of cranial foramina, that ischyromyid and cylindrodontid rodents were very closely related.

A larger, more advanced species of *Pareumys* has been discovered from V-72088. Identification beyond the generic level, however, is impossible with existing material. Design features of the metaloph on the upper molars are nearly perfectly intermediate between those seen in *P. sp.* near *P. grangeri* from San Diego and *P. sp.* near *P. milleri* from younger beds in the Sespe Formation. Whether this intermediacy is indicative of a phylogenetic sequence, however, is unclear and I hesitate to define a new species on such meager information useful in a diagnosis. The material from V-72088 may, indeed, be conspecific with another of the several taxa discussed by Wilson (1940c) but could be unrecognizable because of absence of comparable parts.

The taxa discussed in the present paper indicate that the Friars and Mission Valley for-

mations were deposited within an interval equivalent to the "Uintan" North American Land Mammal Age. Several close comparisons with the preceding "Bridgerian" land mammal age suggest that the San Diego section was emplaced in the earliest parts of the Uintan. It is quite likely significantly older than mammal-bearing localities within the Uintan Hendry Ranch Member of Wyoming that has questionably been placed in the Tepee Trail Formation (see Black, 1974, pp. 151-152) and perhaps can be dated as old as the Bridgerian-Uintan boundary (see Evernden et al., 1964, fig. 1, p. 167). Unfortunately, no radiometric dates are yet available from the Eocene deposits of San Diego County.

The species from V-72088 show many advances over those from the greater San Diego area and have basic similarities with species from the Uintan part of the Sespe Formation; the sediments are probably time-correlative. Correlation of V-72088 with a precise stratigraphic level within the Sespe beds, however, cannot as yet be done. It has long been recognized that the Sespe beds are significantly younger than the Eocene sediments from San Diego (see, for example, Stock, 1948, fig. 3, p. 331).

The southern California Eocene rodent fauna was at first considered to have been quite endemic (see, for example, Black and Dawson, 1966, p. 332). The picture now seems to be changing somewhat, at least for the species list for the San Diego section. As examples: (1) *Microparamys sp.* cf. *M. minutus* is indistinguishable from a Bridgerian species from northeastern Utah; (2) *Sciuravus powayensis* is highly similar to *S. eucristadens* from Bridgerian sediments of northeastern Utah and a close common ancestry is suggested; (3) a possible species of *Griphomys* has recently been discovered in western Wyoming; (4) *Pareumys sp.* near *P. grangeri* is closely similar to *P. grangeri* of the early Uintan Wagonhound beds of northeastern Utah; and (5) *Simimys sp.* has at least been tentatively recognized from the Vieja Group of Trans-Pecos Texas (Wood, 1974, p. 100). Additional faunal similarities are also seen among the marsupials and small ?primates (see Lillegraven, 1976) and other groups as well, not yet documented in the literature. One is now actually hard-pressed to find examples of endemic land

vertebrate genera within the San Diego part of the southern California Eocene section, and the list of species highly similar to or conspecific with those from elsewhere in North America is growing rapidly. Thus widespread overland dispersal across western North America of many species of vertebrates was possible during at least

some part of the earlier Eocene, even in such groups as rodents for which one might expect rather strong edaphic controls on range extension. A more extensive discussion of the Eocene biogeographical relationships between the North American West Coast and the Western Interior is provided by Lillegraven (In press).

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