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New Specimens of *Metanoiamys, Pauromys,* and *Simimys* (Rodentia: Myomorpha) from the Uintan (middle Eocene) of San Diego County, California, and Comments on the Relationships of Selected Paleogene Myomorpha

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ABSTRACT.—The first known mandibular and maxillary specimens of the middle Eocene basal eomyid *Metanoiamys agorus* have been recovered from the Friars Formation (early Uintan) of San Diego County. Although the genus was previously diagnosed as having a horizontal dorsal border of the mandible anterior to p4, this character was based on a specimen that actually pertains to *Microparamys* sp. cf. *M. minutus*. Undoubted mandibles of *M. agorus* are deeply concave anterior to p4, as in all other known eomyids. However, *Metanoiamys* is relatively primitive in that it retains a small P3 (or DP3), has fourth premolars distinctly smaller than the first molars, and has a masseteric fossa that extends only to below the p4–m1 contact.

Pauromys is confidently identified from the Eocene of southern California for the first time, and is currently known in the region only from the lower member of the Stadium Conglomerate (late early Uintan), where it is represented by the new species *P. lillegraveni*. An emended diagnosis of *Pauromys* emphasizing the very small fourth upper and lower premolars suggests that *P. schaubi* Wood and at least part of the hypodigms of *P. exallos* Emry and Korth, *P. texensis* Walton, and *P. simplex* Walton should be excluded from the genus. Since *Pauromys* has lost P3 and has morphologically "myodont" molars, it is here removed from the Sciuravidae and classified as Myodonta, *incertae sedis*.

The abundant southern California late Uintan and Duchesnean rodent *Simimys* has been assumed to have lost P4, leading some workers to link this genus to the Muroidea. However, several new maxillary specimens show that San Diego County late Uintan populations of *Simimys* possessed a tiny, peglike P4 (and/or DP4). The presence of this tooth in the original Sespe Formation species *S. simplex, S. vetus,* and *S. murinus* is uncertain, so specific assignment of the San Diego County material must await recovery of more complete maxillary specimens from the Sespe. The totality of the available evidence suggests that *Simimys* should be classified as Dipodoidea, *incertae sedis.*

INTRODUCTION

Eocene rodents from southern California were first described by R. W. Wilson and Chester Stock in the 1930s and 1940s (see Golz and Lillegraven, 1977, for a complete bibliography). These early collections were obtained from the Sespe Formation of Ventura County (representing the later part of the Uintan and the Duchesnean North American Land Mammal "Ages," NALMAs) and from what is now known as the Friars Formation of San Diego County (early Uintan). See Krishtalka et al. (1987) for a discussion of the Uintan and Duchesnean NALMAs. Later work on the Eocene rodents of southern California was undertaken by Wood (1962), Lindsay (1968), Lillegraven and Wilson (1975), Lillegraven (1977), Chiment (1977), Emry (1981), Walsh (1987, 1991a,b), Mason (1988), Kelly (1990, 1992), Kelly et al. (1991), Kelly and Whistler (1994), and Chiment and Korth (1996).

During the past several years, extensive paleontological monitoring of grading operations in San Diego County has been conducted by PaleoServices, Inc., and the San Diego Natural History Museum. These salvage efforts have produced important new collections of Eocene mammals, various aspects of which were discussed by Walsh (1996). Walsh et al. (1996) provided a reinterpretation of the Friars Formation and Poway Group (Kennedy and Moore 1971) that is critical to understanding the stratigraphic provenance of the Uintan mammals of southwestern San Diego County. The known local stratigraphic ranges of several rodent taxa I discuss are shown in Fig. 1. Such data can help illuminate speculations about ancestral relationships between certain taxa. The purpose of this paper is to describe important new specimens of three genera of myomorph rodents from the Uintan of San Diego County and to discuss the phylogenetic position of these and other selected Paleogene myomorphs.

METHODS

Specimens will often be introduced in the form "XXXX/YYYYY," where "XXXX" represents the locality number and "YYYYY" the specimen number. Some of these localities, various Eocene local faunas, and geographic collecting districts of San Diego County were discussed by Golz and Lillegraven (1977), Walsh (1996), and Walsh et al. (1996). Measurements of teeth were made on an Ehrenreich Photo-Optical Industries "Shopscope" to the nearest 0.01 mm. Measurements of cheek teeth of *Metanoiamys* and *Microparamys* were taken according to the method used by Lillegraven (1977:227). Note that the endpoints for measuring the anterior and posterior widths of the lower cheek teeth of *Metanoiamys* used by Chiment and Korth (1996, following Chiment 1977) yield slightly smaller values than the endpoints used by Lillegraven (1977). Measurements of cheek teeth of *Pauromys* and *Simimys* were taken according to the method used by Lillegraven and

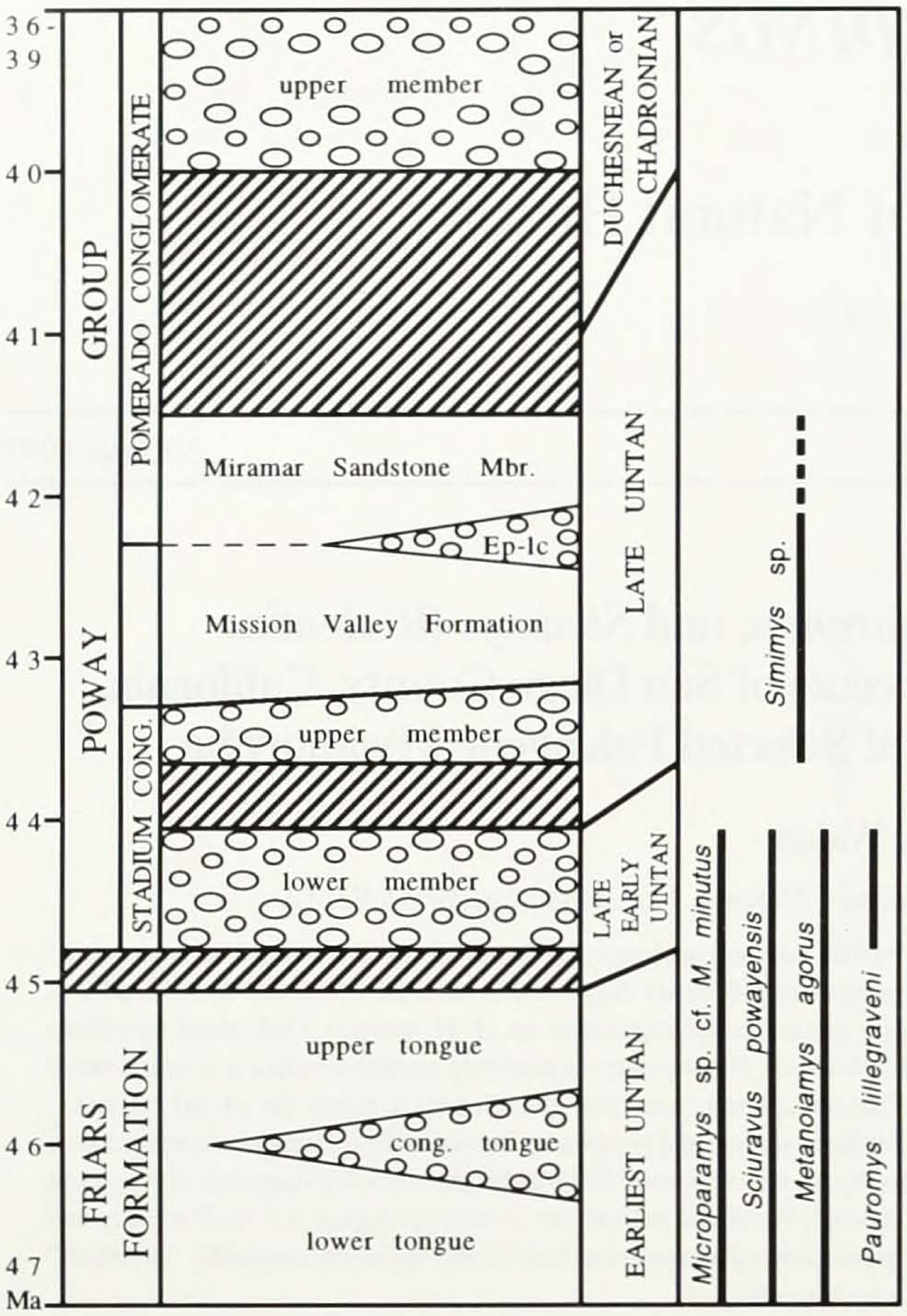


Figure 1. Known lithostratigraphic ranges in southwestern San Diego County of several rodent taxa discussed in this paper. Dashed upper part of the range of *Simimys* sp. represents the inferred extent of its biochronozone. Estimated numerical ages of various units of the Friars Formation and Poway Group are based on information in Walsh (1996), Walsh et al. (1996), and an unpublished new late Duchesnean(?) mammal assemblage from the upper member of the Pomerado Conglomerate. Ep-lc, lower conglomerate member of the Pomerado Conglomerate.

Wilson (1975). Tooth terminology used for *Pauromys* and *Simimys* is largely that of Lillegraven and Wilson (1975). Abbreviations are as follows:

N, sample size.
OR, observed range of variation.
M, arithmetic mean.
SD, standard deviation.
CV, coefficient of variation.
P and M, upper premolar and molar, respectively.
i, p, and m, lower incisor, premolar, and molar, respectively.
D and d, upper and lower deciduous teeth, respectively.
L and R, left and right, respectively.
AP, anteroposterior length of upper and lower teeth.
W, maximum transverse width (for upper premolars of *Pauromys* and *Simimys*).
WTRI, width of trigonid.
WTAL, width of talonid.
AW, anterior width of upper cheek teeth.
PW, posterior width of upper cheek teeth.
AMNH, American Museum of Natural History, New York.
CM, Carnegie Museum of Natural History, Pittsburgh.
CU, University of Colorado Museum of Geology, Denver.
LACM (CIT), original collections of the California Institute of Technology, now housed at the Natural History Museum of Los Angeles County, Los Angeles.
SDSNH, San Diego Society of Natural History.
UCMP, University of California Museum of Paleontology.
USNM, United States National Museum.
YPM, Yale Peabody Museum.

SYSTEMATIC PALEONTOLOGY

Class Mammalia Linnaeus, 1758

Order Rodentia Bowdich, 1821

Suborder Myomorpha Brandt, 1855

Infraorder Geomorpha Thaler, 1966

Family Eomyidae Depéret and Douxami, 1902

Metanoiamys Chiment and Korth, 1996

Known Distribution.—Uintan to Duchesnean (Middle Eocene) of western North America.

Type Species.—Metanoiamys agorus Chiment and Korth, 1996.

Included Species.—Metanoiamys agorus Chiment and Korth, 1996, *M. marinus* Chiment and Korth, 1996, *M. fantasma* (Lindsay, 1968), *M. fugitivus* (Storer, 1984), and *M. lacus* (Storer, 1987).

Emended Diagnosis.—Mouse-sized basal eomyid rodent with generally sciuravid-like cheek teeth (see Chiment and Korth, 1996, for details). Dorsal surface of mandible anterior to p4 deeply concave as in later eomyids, unlike sciuravids. Ridges defining the masseteric fossa converge and terminate anteriorly below the p4-m1 contact, not below p4 as in later eomyids. Linear dimensions of P4/p4 about 10-15% smaller than M1/m1, not subequal to or larger than M1/m1 as in later eomyids. Small P3 retained, not lost as in most later eomyids. No autapomorphies known.

Discussion.—See Korth (1994) for a review and classification of North American Eomyidae. Dawson (1977) and Chiment (1977) showed that specimens from the Sespe Formation of California described by Lindsay (1968) as *Namatomys fantasma* were not congeneric with the type species *Namatomys lloydi* Black, 1965. Subsequently, the unnamed genus was informally referred to as "*Namatomys*" (Storer 1984, 1987, Kelly 1992, Walton 1993). Chiment and Korth (1996) erected the genus *Metanoiamys* to accommodate several species of "*Namatomys*" from the middle Eocene of North America.

In addition to their newly described type species *M. agorus*, Chiment and Korth named another new species, *M. marinus*, based on a small sample of isolated teeth from the latest Uintan or Duchesnean Camp San Onofre local fauna in northwestern San Diego County (see Golz and Lillegraven 1977, Kelly 1990, and Walsh 1996 for discussions of this local fauna). They transferred the late Uintan "*N.*" *fantasma* (Hartman Ranch local fauna) to *Metanoiamys* as well. Walsh (1991b) referred the SDSNH material of *M. agorus* to "cf. *Pauromys* sp.," but the subsequent discovery in 1993 of unequivocal material of *Pauromys* from San Diego leaves no doubt that *Metanoiamys* is indeed generically distinct. Finally, Kelly (1992) described additional isolated teeth of *Metanoiamys* from the Sespe Formation, under the designation of "*Namatomys*" sp., cf. "*N.*" *fantasma*. Chiment and Korth (1996) suggested that Kelly's sample probably pertained to *M. marinus*. In addition to its occurrence in California, *Metanoiamys* has been reported from strata of possibly earliest Uintan age in the Turtle Butte Member of the Bridger Formation (Evanoff et al. 1994), and from the late Uintan and Duchesnean of Saskatchewan (Storer 1984, 1987). Certain specimens from the Uintan of Texas assigned by Walton (1993) to *Pauromys* may also be referable to *Metanoiamys* (see below).

Chiment and Korth (1996, fig. 1a) based part of the diagnosis of *Metanoiamys* on a mandible with i1 and alleged dp4 (UCMP V-71211/96399; Figs. 2B, 2D). The cheek tooth in this mandible, however, is a permanent, not deciduous, premolar, and the specimen actually pertains to the slightly larger rodent *Microparamys* sp. cf. *M. minutus*, isolated teeth of which were previously described by Lillegraven (1977). The mandible of UCMP 96399 differs from those of *Metanoiamys agorus* (e.g., SDSNH 50590; Figs. 2A, 2C) in its deeper ramus, larger incisor (Table 1), and notably stronger masseteric ridges. The masseteric fossa in UCMP 96399 extends anteriad to below the m1-m2 contact, while the anterior edge of the most anterior ridge that defines the fossa extends to below the middle of m1. The anterior extent of the masseteric fossa in UCMP 96399 matches that in *Microparamys tricus* and *M. dubius* (Wilson 1940a, Dawson 1966). The masseteric fossa, however, does not extend as far forward as in the undoubted mandibles of *Metanoiamys* described below.

On the basis of UCMP 96399, Chiment and Korth (1996) included in the diagnosis of *Metanoiamys* the presence of a distinct ridge extending across the horizontal diastema from immediately anterior to p4 to just posteriad of the incisor alveolus (Fig. 2B). This ridge seems to be a primitive "protrogomorph" character. A similar ridge is present in the holotype of *Microparamys tricus* (LACM [CIT] 1122; Wilson 1940a), the holotype of *Reithroparamys delicatissimus* (AMNH 12561; Wood 1962), several SDSNH specimens of *Pseudotomus littoralis* and *P. californicus*, and various species of *Paramys*. It is also present but weaker in *Sciuravus* and *Pareumys*. The ridge is absent, however, in the three known mandibles of *Metanoiamys agorus* described below (e.g., SDSNH 50590, Fig. 2A), and the diastema is markedly concave, not horizontal as in UCMP 96399.

The p4 in UCMP 96399 is unlike that of *Metanoiamys agorus* but typical of *Microparamys* sp. cf. *M. minutus* in having a weaker protoconid, a weaker mesostylid, a lower but more continuous and more posteriorly situated posterolophid, and a relatively smaller entoconid and hypoconid that are located at the extreme posterior corners of the crown. The p4 in UCMP 96399 is also larger in absolute size (AP 1.13 mm, WTAL 1.04 mm) than all but one known p4 of *Metanoiamys agorus* (UCMP 109876). That the premolar in UCMP 96399 is a permanent p4 is demonstrated by its occlusal outline's being compressed anteroposteriorly relative to undoubted dp4s of *Microparamys* sp. cf. *M. minutus*. Given these observations, one other p4 listed by Chiment and Korth (1996:117) pertains to *Microparamys* sp. cf. *M. minutus* (UCMP V-72157/109615; AP 1.23 mm, WTAL 1.07 mm.). Fortunately, the first known mandibles and maxillary fragments of *Metanoiamys* have recently been collected from San Diego, allowing a revised diagnosis and a reevaluation of the phylogenetic position of this rodent.

TABLE 1. Mandibular depth below m1, and dorsoventral lengths and transverse widths of lower incisors of *Microparamys*, *Metanoiamys*, *Pauromys*, and *Simimys* from the Uintan of San Diego County, California. Measurements in mm.

	Mandibular depth	i1 length	i1 width	width/ length
Microparamys sp. cf. *M. minutus*				
UCMP V-71211/96399	3.8	1.65	0.83	0.50
Metanoiamys agorus				
SDSNH 3784/49385	3.5	—	—	—
SDSNH 3784/50590	3.5	1.02	0.59	0.58
Pauromys lillegraveni				
SDSNH 3691/46501	3.4	1.20	0.68	0.57
Simimys sp.				
SDSNH 3564/47100	3.3	1.21	0.66	0.55
SDSNH 3564/47807	3.4	—	—	—
SDSNH 3870/54610	3.4	1.25	0.66	0.53
SDSNH 4019/60065	3.3	—	—	—

Metanoiamys agorus Chiment and Korth, 1996

Figs. 2A, 2C, 3, 5

Holotype.—UCMP 106432, an isolated dp4 (not p4 as indicated by Chiment and Korth 1996).

Type Locality.—UCMP V-72157, "Poway Pipeline One," Rancho de los Peñasquitos district, San Diego County, upper tongue of Friars Formation.

Known Distribution.—Earliest Uintan to late early Uintan of San Diego County, California. Friars Formation, Member B of Santiago Formation, and lower member of Stadium Conglomerate. All UCMP localities assigned by Chiment and Korth (1996) to the Mission Valley Formation actually pertain to the upper tongue of the Friars Formation (Walsh 1996, Walsh et al. 1996).

Diagnosis.—See dental diagnosis of *M. agorus* given by Chiment and Korth (1996:118).

Referred Material.—SDSNH 49385 (mandible fragment with p4-m3) and SDSNH 50590 (associated mandible with i1 + p4-m1 and maxilla fragment with M1-3), both from SDSNH Loc. 3784, Friars Formation. SDSNH 49630 (maxillary fragment with alveolus for P3 and complete P4-M1), from SDSNH Loc. 3789, Friars Formation. SDSNH 56201 (mandible fragment with i1 + p4-m2), from SDSNH Loc. 3824, conglomerate tongue of Friars Formation. In addition, about 1683 isolated teeth are known from 46 different SDSNH localities in the Friars Formation, 226 isolated teeth are known from Member B of the Santiago Formation (SDSNH Locs. 3440, 3443, 3448, 3450, 3465, and 3571; Mesa Drive local fauna of Walsh 1996), and 3 isolated teeth are known from the lower member of the Stadium Conglomerate (SDSNH Loc. 3691, Murray Canyon local fauna of Walsh 1996).

Mandible and Lower Incisor.—Three mandibular fragments of *M. agorus* are now available, two of which are complete enough to show the sciurognathous condition of the angle (SDSNH 49385, 50590). The relatively weak ridges defining the masseteric fossa converge and terminate below the p4-m1 contact (Fig. 2C). The ventral ridge is slightly stronger than the dorsal ridge. The diastema is deeply concave in SDSNH 50590 (Fig. 2C). This region is damaged in SDSNH 49385 and 56201 but seems to have been distinctly concave in these specimens as well. On SDSNH 50590 and 56201, there is a single mental foramen on the lateral side of the mandible, ventral and well anterior to p4 (this area is broken away on 49385). A small keel is present on the ventral side of the mandible below the diastema on SDSNH 50590 (the other two mandibles are damaged in this area). On SDSNH 49385 and 50590, the coronoid begins to ascend from the body of the ramus at the level of the m2 talonid, and both mandibles possess two small foramina between m3 and the ascending ramus. There is a distinct "pocket" in the dorsal surface of the mandible posterior to m3, bounded laterally by the ascending ramus and medially by a distinct ridge running posteriad from the posterior root of m3. The depth of both measurable mandibles below m1 is 3.5 mm (Table 1). Unlike the condition in *Pauromys* and *Simimys* (see below), there is no prominent anteroposteriorly elongate bulge on the medial face of mandible below p4-m1 (Fig. 3A).

Only SDSNH 50590 preserves a complete lower incisor (Figs. 2A, 2C, 3A). It is smaller and not as tranversely compressed as that of *Microparamys* sp. cf. *M. minutus* (Table 1). The ventral face is distinctly convex, the lateral face is slightly convex, and the medial

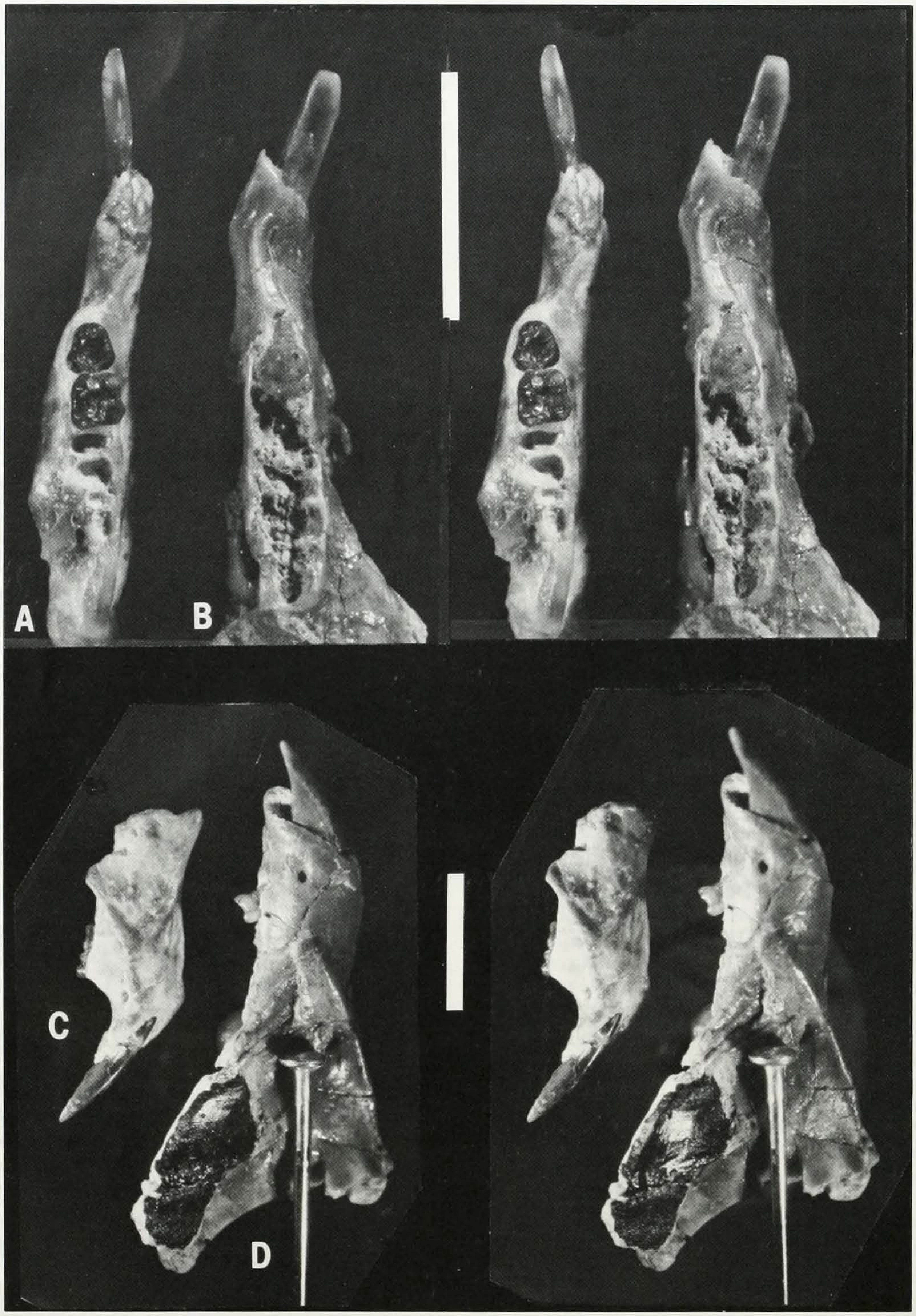


Figure 2. Stereophotographs of (A), SDSNH 50590, L mandible of *Metanoiamys agorus* with i1 + p4–m1, occlusal view; (B), UCMP 96399, R mandible of *Microparamys* sp. cf. *M. minutus* with i1 + p4, occlusal view; (C), SDSNH 50590, lateral view; (D), UCMP 96399, lateral view. Scale bars = 5 mm.

face is nearly flat. The enamel is ungrooved, extending about one-third of the way onto the lateral face and only a very short distance onto the medial face. A small narrow pulp cavity is present.

Lower Premolars.—SDSNH 49385 preserves p4–m3 (Fig. 3B) and confirms the original description of the lower tooth row based on isolated teeth (Chiment and Korth 1996). Measurements of cheek teeth of *Metanoiamys agorus* preserved in mandibular and maxillary fragments are given in Table 2. Chiment and Korth (1996:117) identified eight lower premolars of *M. agorus* as deciduous, nine as permanent, and 23 as "deciduous or permanent" (although their table 1 listed 17 dp4s and 21 p4s). Some lower premolars of *M. agorus* are indeed difficult to allocate, but most fall into two distinct morpho-

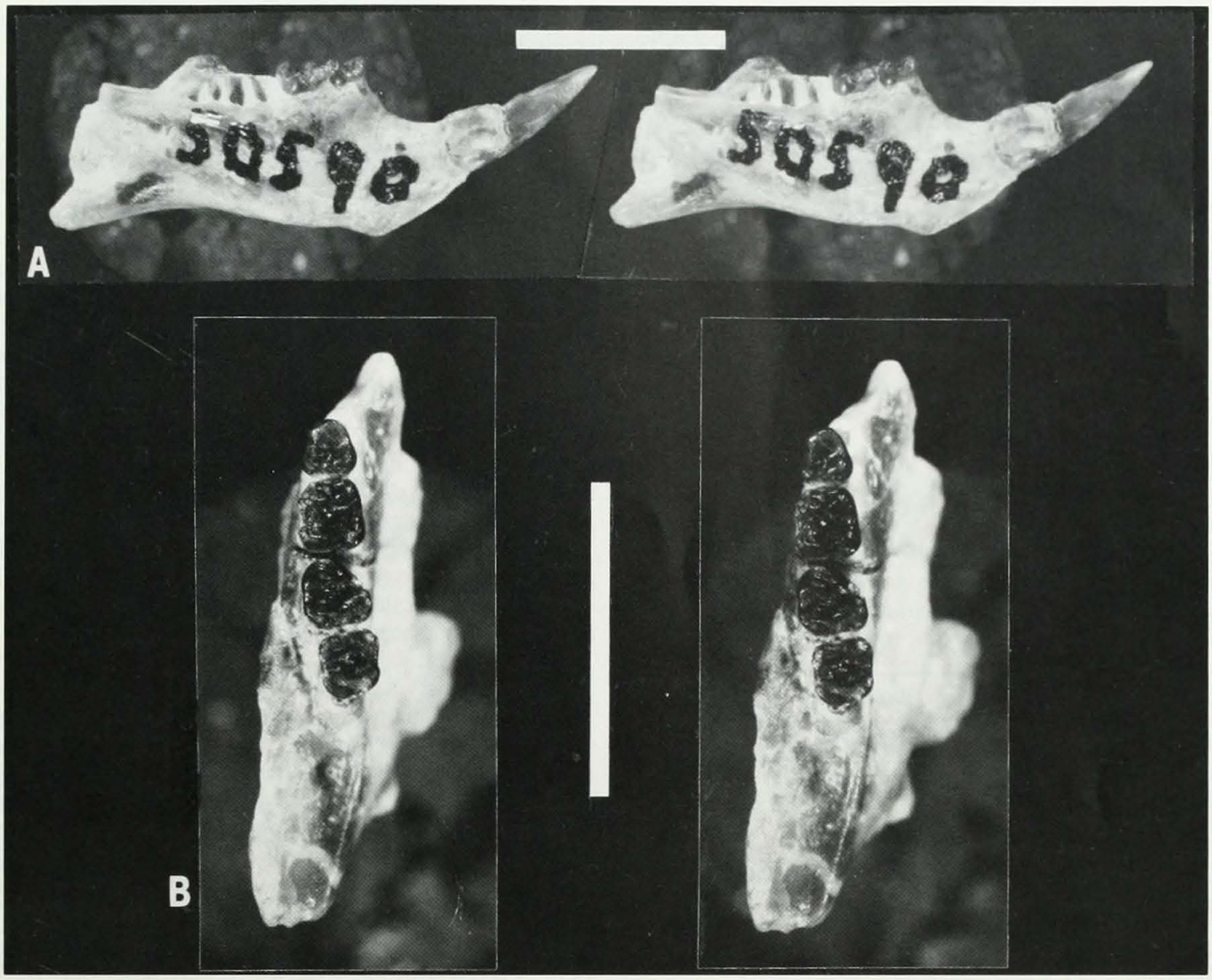


Figure 3. Stereophotographs of (A), SDSNH 50590, L mandible of *Metanoiamys agorus* with i1 + p4–m1, medial view, (B), SDSNH 49385, L mandible of *Metanoiamys agorus* with p4–m3, occlusal view. Scale bars = 5 mm.

logical categories. One morph is a relatively small anteroposteriorly elongated tooth with a relatively narrow talonid and usually with a tiny anteroconid. This morph is represented by the holotype specimen UCMP 106432, which Chiment and Korth (1996, fig. 1C) identified as p4. The other morph is a relatively equant tooth, with a relatively wide talonid and usually with a weaker or absent anteroconid. This morph is represented by UCMP 109949, which Chiment and Korth (1996, fig. 1B) identified as dp4. From the following evidence, however, the more equant morph actually pertains to p4, and the anteroconid-bearing elongate morph to dp4.

As seen in *Microparamys*, *Sciuravus* (Dawson 1968; Lillegraven 1977), *Pareumys* (Lillegraven 1977), a variety of ischyromyid rodents (Wood 1962), and the eomyids *Adjidaumo* and *Yoderimys* (Wood 1937, fig. 49; Emry and Korth 1993, figs. 1-5; 1-6), dp4 is always a relatively long and narrow tooth, more molariform than p4, usually with a stronger anterior cingulid and/or anteroconid. The same pattern holds for *Metanoiamys*, in which the anteroconid on dp4 complements the anterocone on DP4 and the relatively long dp4 complements the relatively long DP4. The relatively elongate morph usually has resorbed roots, as expected for a deciduous tooth, whereas the more equant morph more often has intact, relatively robust roots, as expected for a permanent tooth. Conclusive evidence that the more equant morph represents the permanent p4 in *Metanoiamys* is seen in SDSNH 49385, 50590, and 56201, all mandibles having relatively equant, lightly worn premolars in place with equally worn or more heavily worn molars. In addition, SDSNH 56201 contains an equant premolar with long, robust roots and no sign of an unerupted premolar below it. Accordingly, the lower premolars of *Metanoiamys agorus* studied by Chiment and Korth (1996) are reidentified as follows (asterisks indicate UCMP specimens included in Table 3 and Figure 4):

dp4: UCMP 99201, 101288*, 101564*, 106060*, 106260*, 106800*, 106905*, 106925*, 109914, 109765*, 110170*.

p4: UCMP 96262*, 96389, 101138*, 101157*, 101202, 101207*, 101280, 104588*, 106254*, 106427*, 106449*, 106450, 106823*, 106922*, 109615, 109635*, 109762, 109876*, 109949*, 110221, 110254*.

p4 or dp4: UCMP 101190, 101139, 105964, 106265, 106827, 106832, 110220.

Given the removal of two relatively large p4s of *Microparamys* sp. cf. *M. minutus* from the original hypodigm of *M. agorus*, and given that most teeth identified by Chiment and Korth (1996) as dp4s are actually p4s (and vice versa), the statistics for the lower premolars of *M. agorus* provided by these authors are not meaningful. Therefore, I remeasured AP and WTAL on the confidently reidentified complete lower premolars in the original hypodigm. To these were added measurements of a new sample of lower premolars of *M. agorus* from several SDSNH localities in the upper tongue of the Friars Formation. The resulting statistics for this combined sample

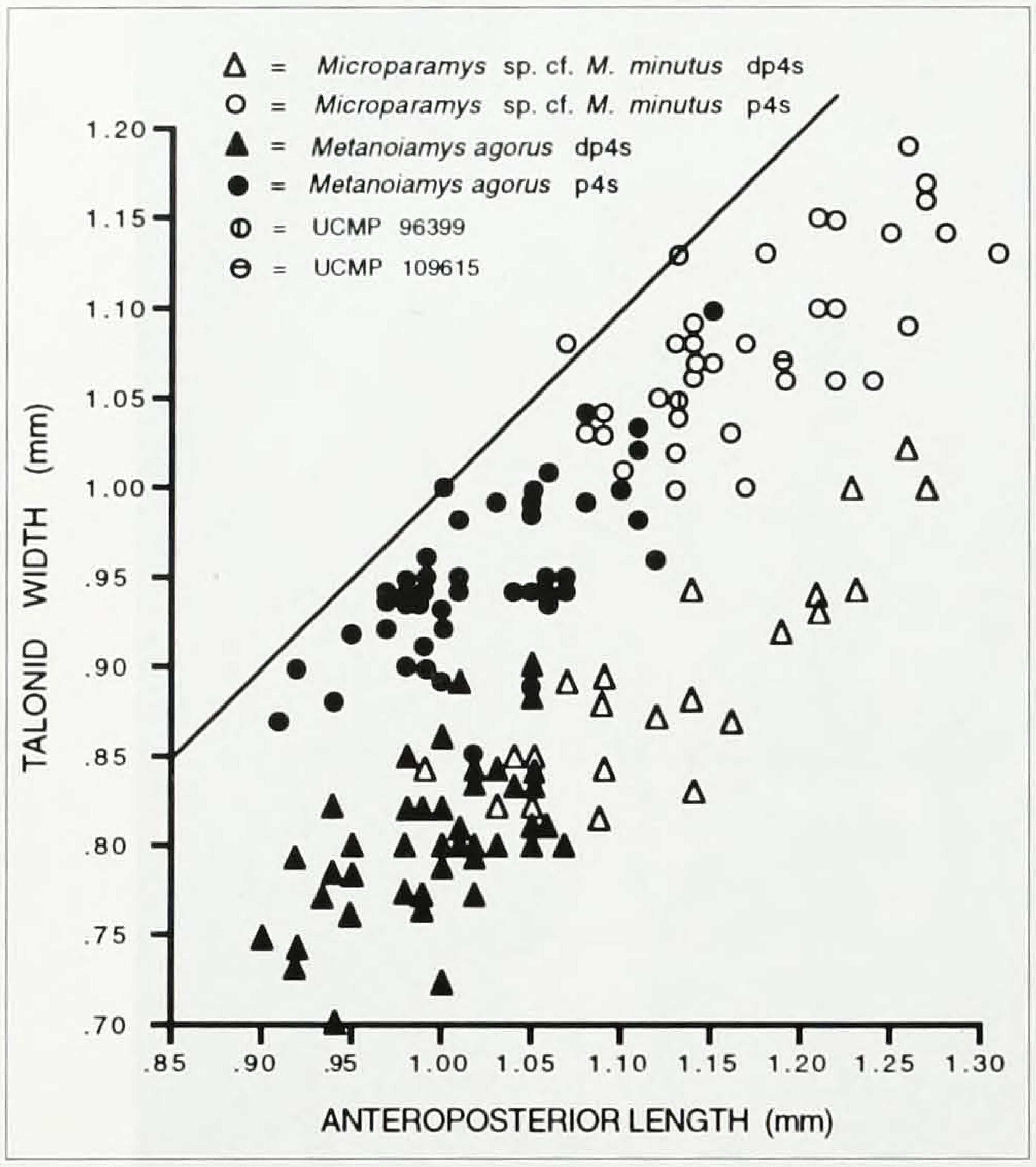


Figure 4. Anteroposterior length versus talonid width for permanent and deciduous lower premolars of *Metanoiamys agorus* and *Microparamys* sp. cf. *M. minutus*. Note slight overlap in size ranges of each category and the distinctly smaller average size of the *Metanoiamys* premolars. Specimen numbers of teeth represented are given in Tables 3 and 4.

are given in Table 3.

A pooled sample of lower premolars of *Microparamys* sp. cf. *M. minutus* from several SDSNH localities from all lithostratigraphic subdivisions of the Friars Formation was also measured (Table 4) to quantify the metric differences between the two species better. Bivariate plots of the data used to compile Tables 3 and 4 are illustrated in Fig. 4. Although a slight overlap is evident, the four categories cluster at distinctly different regions on the graph. Note that for both species p4 tends to be more equant (plot closer to the line of equal length and width) than dp4.

Maxillae and Upper Premolars.—Two maxillary fragments of *M. agorus* are now available. SDSNH 50590 (not figured) contains M1-3 and confirms the original description of the upper molars based on isolated teeth (Chiment and Korth 1996) but preserves no other relevant characters. SDSNH 49630 (Fig. 5) preserves an empty alveolus at the P3 locus plus complete, unworn P4-M1. SDSNH 49630 is barely complete enough to show that the posterior edge of the inferior zygomatic root originated anterolateral to P3. In contrast to the condition in *Pauromys* and *Simimys* (see below), there was no distinct knob for the insertion of the masseter lateralis superficialis immediately anterior to P3, but not enough of the maxilla is preserved to determine whether such a knob was present immediately ventral to the infraorbital foramen as in *Paradjidaumo* and *Aulolithomys* (Wood 1974:74).

Although the empty P3 alveolus in SDSNH 49630 is relatively large, it seems to be somewhat damaged, and P3 (and/or DP3) was presumably single-rooted, with a small crown of unknown morphology. The presence of DP3 in juveniles of *M. agorus* is established by the occurrence of small, often very subtle, anterior appression facets on 24 of the 80 DP4s in SDSNH collections for which the status of this feature can be determined. (e.g., SDSNH 43030, 43175, and 51002). *Contra* Chiment and Korth (1996:117), two DP4s in the original hypodigm also have such a facet (UCMP 99202 and 106669). That adults of *M. agorus* possessed a tooth in the P3 locus is shown by small anterior appression facets on 47 of 104 determinable P4s in SDSNH collections (e.g., SDSNH 39221, 43186, and 51007). *Contra* Chiment and Korth (1996:117), four P4s in the original hypodigm also have such a facet (UCMP 96256, 96328, 96478, and 101177). Whether the tooth in the P3 locus in adult animals is a retained DP3 or a permanent P3 is uncertain.

The inconsistent occurrence of anterior appression facets on P4/DP4 of *Metanoiamys agorus* is probably attributable to (1) death of some individuals prior to full eruption of the premolars and (2) slight individual variations in the relative positions of DP3/DP4 and P3/P4. This conclusion is supported by the evidence seen in isolated premolars of *Sciuravus powayensis* (see Wilson 1940b, Lillegraven 1977). Even though this species is known to possess a DP3 replaced by a permanent P3, only 23 of 33 determinable DP4s and 17 of 46 determinable P4s in SDSNH collections have a detectable anterior facet.

It should be noted that eight of the M3s referred by Chiment and Korth (1996:118) to *Metanoiamys agorus* actually pertain to *Microparamys* sp. cf. *M. minutus* (UCMP 96258, 96267, 96402, 101281, 106861, 109565, 109815, and 110219). These teeth are larger than M3s of *Metanoiamys agorus*, often have crenulated enamel and taller paracones, and are generally more anteroposteriorly elongated. Finally, UCMP 99343 does not pertain to *M. agorus* but is a heavily damaged M3 probably referable to *Sciuravus*.

Discussion.—The presence of a P3 alveolus in SDSNH 49630, together with the presence of frequent appression facets on the anterior faces of isolated DP4s and P4s, clearly shows that the early Uintan species *Metanoiamys agorus* retained the primitive rodent condition of possessing two upper premolars. Lindsay (1968) described P4s of the late Uintan Sespe Formation species *M. fantasma* as lacking an anterior appression facet. Of the 12 determinable P4s of this species from UCMP V-5814, however, 7 have small but

TABLE 2. Measurements (mm) of cheek teeth of *Metanoiamys agorus* in maxillary and mandibular fragments.

	P4			M1			M2			M3		
	AP	AW	PW	AP	AW	PW	AP	AW	PW	AP	AW	PW
SDSNH 49630	1.03	1.04	1.03	1.19	1.17	1.22	—	—	—	—	—	—
SDSNH 50590	—	—	—	1.09	1.16	1.21	1.10	—	—	0.92	1.02	—

	p4			m1			m2			m3		
	AP	WTRI	WTAL	AP	WTRI	WTAL	AP	WTRI	WTAL	AP	WTRI	WTAL
SDSNH 50590	0.99	0.77	1.00	1.13	1.01	1.09	—	—	—	—	—	—
SDSNH 49385	0.90	0.73	0.91	1.12	1.02	1.10	1.14	—	1.13	1.08	1.01	0.95
SDSNH 56201	1.00	0.78	1.00	1.09	0.90	0.91	1.15	1.08	1.11	—	—	—

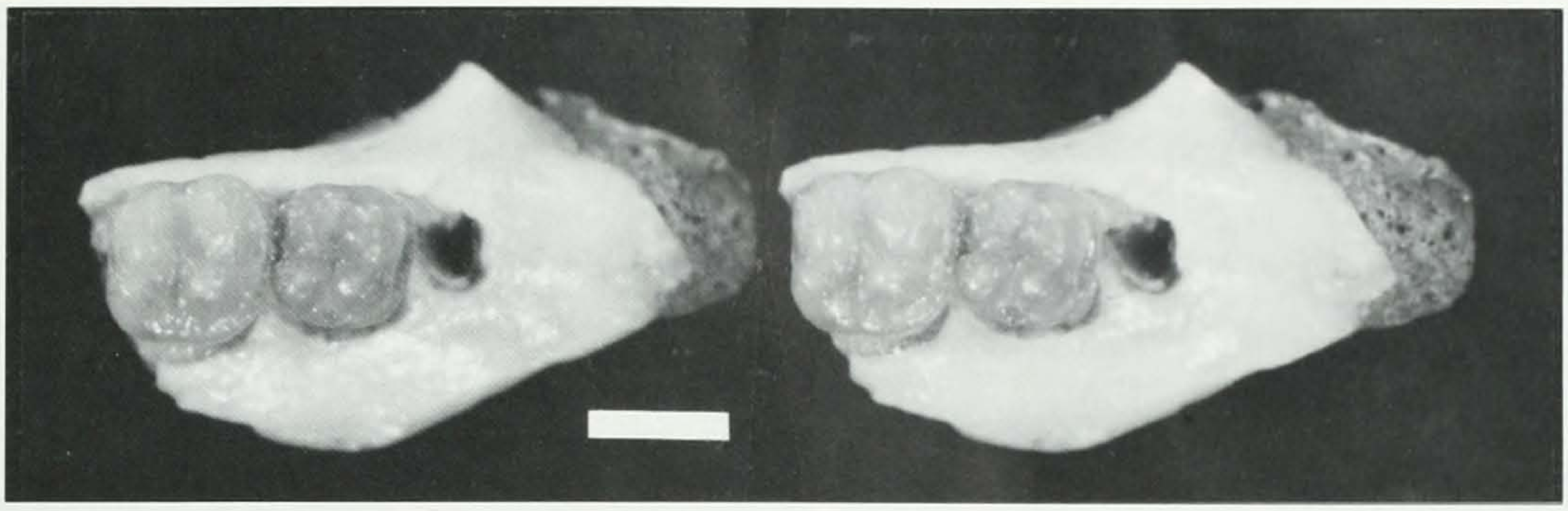


Figure 5. Stereophotograph in occlusal view of SDSNH 49630, R maxillary fragment of *Metanoiamys agorus* with alveolus for P3 (or DP3) + P4–M1. Scale bar = 1 mm.

distinct anterior facets, indicating the presence of P3 and/or DP3 (UCMP 77648–77650, 77652, 91685–91686, and 116482). The sole DP4 from this locality also has a faint anterior facet (UCMP 79504). No P4s or DP4s are present in the recently collected Tapo Canyon and Brea Canyon samples of isolated teeth of *Metanoiamys* described by Kelly (1992). Finally, of the five P4s and one DP4 of *Metanoiamys marinus* from V-72088, none has an unequivocal anterior facet. More complete material must be collected from the superposed local faunas of the Sespe Formation for the persistence of P3/DP3 in this genus from late Uintan to Duchesnean time to be evaluated.

When the first species of *Metanoiamys* was described from the late Uintan of southern California (under the name *Namatomys fantasma*), Lindsay (1968) suggested it may have been derived from the early Uintan rodent *Sciuravus powayensis*. As discussed by Storer (1987), however, the origin of *Metanoiamys* is more likely to be found among Wasatchian-Bridgerian species of the sciuravid *Knightomys*. Indeed, upper molars from the Wasatchian of New Mexico assigned by Flanagan (1986) to *K. reginensis* appear to be quite similar in size and morphology to those of *M. agorus*, and the collection of complete mandibles and maxillaries of *K. reginensis* is awaited.

On the basis of its presumed lack of P3, Storer (1987) assumed that the Uintan *Metanoiamys* could not be ancestral to the aberrant Chadronian eomyid *Yoderimys*, which retains P3 (Wood 1974). He therefore suggested that the stem eomyid must be of Bridgerian age. The documented presence of P3 in *Metanoiamys*, however, now removes all objections to this genus as representing the basal eomyid morphotype. Another primitive sciuravid character of *Metanoiamys* is the distinctly smaller size of p4 and P4 relative to m1 and M1. In *Yoderimys* and later eomyids, the premolars are subequal to or larger than the first molars (Wood 1974, Emry and Korth 1993). Despite these primitive retentions, the dorsally concave mandibular diastema is a derived character linking *Metanoiamys* with later eomyids (e.g., *Aulolithomys* and *Viejadjidaumo*; Wood 1974). More complete material will be required to determine if *Metanoiamys* had already evolved the sciuromorphous zygomasseteric structure typical of later members of the family (e.g., Wood 1974).

Infraorder Myodonta Schaub, 1958

Myodonta *incertae sedis*

Pauromys Troxell, 1923

Type Species.—Pauromys perditus Troxell, 1923.

Included Species.—Pauromys perditus Troxell, 1923, *Pauromys* sp. [unnamed Powder Wash species; Dawson 1968], and *P. lillegra-*

TABLE 3. Statistics for lower premolars of *Metanoiamys agorus*, based on reidentified specimens from original UCMP hypodigm, combined with sample from several SDSNH localities in the upper tongue of the Friars Formation (Rancho Peñasquitos and Carmel Mountain Ranch districts).[a]

	dp4		p4	
	AP	WTAL	AP	WTAL
N	48	47	45	45
OR	0.90–1.07	0.70–0.90	0.91–1.15	0.85–1.10
M	0.99	0.80	1.02	0.95
SD	0.044	0.046	0.055	0.049
CV	4.5	5.7	5.4	5.2

[a] SDSNH specimens measured, dp4s: **Loc. 3254:** 26909, 26919, 26960, 26983, 26991, 27125, 27684, 27722, 27736, 27055. **Loc. 3391:** 32562, 32571, 32572, 32584, 32612. **Loc. 3482:** 37654. **Loc. 3483:** 39013–39015, 39017–39020, 39022, 39023, 39025–39029, 39031–39033, 39035–39038. **Loc. 3771:** 47271, 47274, 47275.
p4s: **Loc. 3254:** 26897, 26898, 26900, 26964, 27735. **Loc. 3373:** 31423, 31429, 31439, 31433, 31447. **Loc. 3391:** 32564, 32589, 32601, 32608, 32618, 32621. **Loc. 3482:** 37655, 37658. **Loc. 3483:** 39039, 39041–39046, 39051–39053, 39055, 39057. **Loc. 3771:** 47277.

TABLE 4. Statistics for lower premolars of *Microparamys* sp. cf. *M. minutus*, based on sample from several SDSNH localities in all lithostratigraphic subdivisions of the Friars Formation.[a]

	dp4		p4	
	AP	WTAL	AP	WTAL
N	22	22	34	34
OR	0.99–1.27	0.81–1.02	1.07–1.31	1.00–1.19
M	1.13	0.89	1.18	1.08
SD	0.080	0.082	0.065	0.051
CV	7.1	6.9	5.5	4.7

[a] Specimens measured, dp4s: **Loc. 3254:** 26901. **Loc. 3373:** 31564. **Loc. 3391:** 32600. **Loc. 3414:** 41319. **Loc. 3482:** 37624. **Loc. 3483:** 38785, 38787, 38790, 38792. **Loc. 3494:** 37402. **Loc. 3591:** 43962. **Loc. 3611:** 45920–45922. **Loc. 3617:** 43101, 43102. **Loc. 3621:** 58037, 58038. **Loc. 3655:** 46156, 46157. **Loc. 3656:** 46298, 46299.
p4s: **Loc. 3254:** 26903. **Loc. 3373:** 31413, 31544, 31545, 31549, 31565. **Loc. 3380:** 42441. **Loc. 3483:** 38793, 38794, 38798–38801, 38803–38805. **Loc. 3611:** 45176. **Loc. 3612:** 45563, 45565. **Loc. 3883:** 55691, 55692. **Loc. 3616:** 43011. **Loc. 3621:** 58039–58041, 58043, 58044. **Loc. 3655:** 46158, 46159, 46161, 46301. **Loc. 3658:** 45839. **Loc. 3893:** 55176, 55313.

veni sp. nov.

Known Distribution.—Early Bridgerian of the Green River Formation, Utah. Early or late Bridgerian of the Bridger Formation, Wyoming. Early Uintan of the Adobe Town Member of the Washakie Formation, Wyoming (M. R. Dawson, pers. comm.). Late early Uintan of the lower member of the Stadium Conglomerate, California. Questionably known from the Bridgerian of Nevada (Emry and Korth 1989), and the Uintan of Texas (Walton 1993) and Utah (Walsh 1996, table 4).

Emended Diagnosis.—Mouse-sized basal myodont rodent. Molars of generalized myodont construction. Dorsal surface of mandible virtually horizontal anterior to p4 but without distinct ridge as in *Sciuravus*, *Microparamys*, and other ischyromyids. Ridges defining the masseteric fossa extend anteriorly to below the m1 talonid. Derived with respect to *Armintomys* in the loss of P3 and the reduction of P4/p4. Primitive with respect to *Simimys*, *Elymys*, *Pappocricetodon*, and *Nonomys* in retaining a three-rooted P4 (although with an anteroposterior length only about 50% of M1), a p4 (although with an anteroposterior length only about 50% of m1), and having a relatively wider m1 trigonid. No autapomorphies known.

Pauromys lillegraveni sp. nov.
Figs. 6, 7A

Holotype.—SDSNH 46501, L mandible fragment with i1 + p4–m3.

Type Locality.—SDSNH Loc. 3691, "Murray Canyon 1," lower member of Stadium Conglomerate.

Known Distribution.—Lower member of the Stadium Conglomerate (late early Uintan), San Diego County, California.

Etymology.—Species named for Dr. Jason A. Lillegraven, for his contributions to vertebrate paleontology.

Diagnosis.—Lower p4 comparable in absolute and relative size to that of *P. perditus*, averaging distinctly smaller than that of *P.* sp. from Powder Wash. Lower p4 roots completely fused at level of alveolar border, not separate as in *P. perditus*. Lower p4 with single trigonid cusp (no metaconid), unlike *P. perditus* and *P.* sp. from Powder Wash. Lower p4 with no ectolophid or mesoconid, unlike *P.* sp. from Powder Wash. Entoconids of m1-2 conical, not anteroposteriorly compressed as in *P. perditus*. Length of m3 averaging shorter than m1 and m2, apparently unlike *P. perditus* and *P.* sp. from Powder Wash.

Referred Material.—SDSNH Loc. 3691: SDSNH 47708-47709, p4s. 46530-46532, m1s. 46533, m3. 47710, P4. 46502, maxilla fragment with P4-M1. 46535, M1. 46503 and 46534, M2s. 46536, M3.

SDSNH Loc. 3701: SDSNH 48011-48012, m1s. 48016, m2. 48013, M1.

SDSNH Loc. 3731: SDSNH 56685, P4. 56686, M1. 56687, M2 fragment.

Mandible and Lower Incisor.—The holotype mandible shows the sciurognathous condition of the angle (Fig. 6B). The relatively weak ridges defining the masseteric fossa converge and terminate below the m1 talonid (Fig. 6C). The ventral ridge is slightly stronger than the dorsal ridge. A single mental foramen is present at the dorsoventral midpoint of the lateral side of the mandible, directly below the anterior edge of the root of p4. The diastema anterior to p4 is virtually horizontal but lacks the distinct ridge present in *Microparamys*, *Sciuravus*, and a variety of ischyromyid rodents (Fig. 6A). The coronoid process begins to ascend from the dorsal border of the ramus at about the middle of m3, as in *Simimys* (and not at the level of the middle of m2 as in *Metanoiamys*). As in *Simimys* (see below), there is a single foramen between m3 and the ascending ramus (obscured by matrix in Fig. 6A). An apparently similar foramen in *Plesiosminthus myarion* was identified by Schaub (1930, fig. 9) as an opening for the mandibular canal. Unfortunately, the other two known mandibles of *Pauromys* (YPM 13601 and CM 19568) are damaged in this area. Also as in *Simimys*, there is a prominent anteroposteriorly elongated bulge on the medial face of the mandible below m1, p4, and the posterior part of the diastema (Fig. 6B). With two minor exceptions, the mandible of SDSNH 46501 agrees closely in all comparable characters with CM 19568, the edentulous mandible from Powder Wash assigned by Dawson (1968) to *Pauromys* sp. The ventral keel noted by Dawson (1968) on CM 19568 is better developed than on SDSNH 46501, while the mental foramen on CM 19568 occurs slightly higher on the mandible than it does in SDSNH 46501.

SDSNH 46501 preserves a complete lower incisor (not figured). The tip was broken off during the screen-washing process and was picked out separately but has not been reattached. The ventral face is distinctly convex, the lateral face is slightly convex, and the medial face is very slightly convex. The enamel is ungrooved, extending about one-fourth of the way onto the lateral face and only a very short distance onto the medial face. A small narrow pulp cavity is present. The lower incisor of *Pauromys lillegraveni* is similar in proportions to that of *Metanoiamys agorus* but distinctly larger, and very similar in proportions and size to the lower incisor of *Simimys* sp. (Table 1).

Lower Cheek Teeth.—The lower cheek teeth of *Pauromys lillegraveni* are similar in proportions and general morphology to those of *P. perditus* (see Troxell 1923, fig. 1; Dawson 1968, figs. 39-40). Three p4s are known, all of which are much smaller than m1 (Table 5). The p4 in the holotype mandible is well worn (Fig. 6A), but the two isolated p4s are unworn, and both show only a single small trigonid cusp. This condition differs from that in *Pauromys perditus* and *P.* sp. from Powder Wash, in which both the protoconid and metaconid are reportedly present on p4 (Dawson 1968:358). All three teeth are rounded and subtriangular in occlusal outline. The median valley is anteriorly concave and has no accessory cuspules or lophids. The hypoconid and entoconid are subequal in size, conical, and connected to one another by an anteriorly concave hypolophid. A short posterior cingulid is present only on SDSNH 47709. There is only a single trunk root of p4 visible above the alveolar border in SDSNH 46501, although a slight constriction on the labial face of the root suggests the possibility of a partial ventral bifurcation. Nevertheless, the condition of the p4 root in SDSNH 46501 differs from that seen in the type mandible of *P. perditus*, in which two distinct roots are present immediately below the crown (Dawson 1968, fig. 40).

Six complete m1s are known, although SDSNH 48011 is too worn to show any significant details of the crown. Distinct appression facets on the anterior faces of the five isolated m1s preclude their identification as *Simimys*. The metaconid is always essentially conical and lacks a metalophulid. A weak lingual lophid extends from the posterior face of the metaconid to the metastylid region on all five determinable m1s. A weak transversely compressed metastylid is present at the posterior end of the lingual lophid on all four determinable m1s. The entoconid is usually slightly elongated transversely and is subequal to the metaconid. A moderately strong postprotocristid is present on all five determinable m1s. In all three unworn m1s, the postprotocristid extends only about halfway up the posterior face of the metaconid. The unworn m1s have a weak but transversely elongate anteroconid, which assumes the morphology of an anterior cingulid with wear. There is no preprotocristid connecting the protoconid with the anterior cingulid. There are no prominent lingual or labial mesolophids on any m1 (unlike many teeth of *Simimys*), so the term mesoconid is used for the entirety of the small, usually slightly transversely elongate ridge present in the labial half of the median valley. The mesoconid is connected to the hypoconid by a short posterior ectolophid in three of four determinable m1s; in the remaining m1, the mesoconid is small, conical, and isolated. The hypoconid is subequal to the protoconid and entoconid and is conical to slightly anteroposteriorly compressed. A weak hypolophid connects the hypoconid with the hypoconulid in all five determinable m1s; there is never a direct connection between the

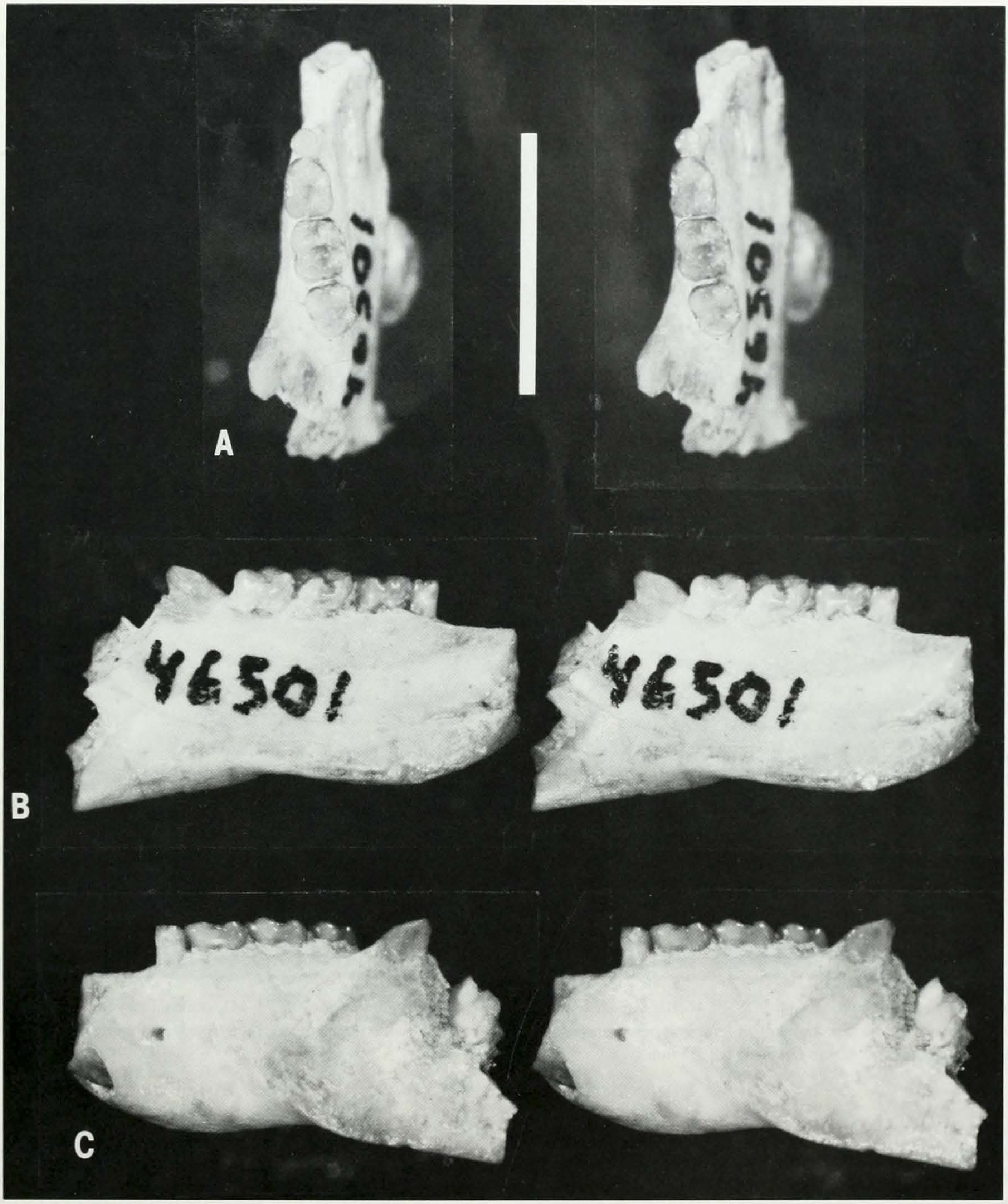


Figure 6. Stereophotographs of SDSNH 46501, holotype L mandible of *Pauromys lillegraveni* with i1 + p4–m3: (A), occlusal view; (B), medial view; (C), lateral view. Scale bar = 5 mm.

hypoconid and entoconid. The hypoconulid is a weak to moderate swelling of the short posterior cingulid. A very narrow labial shelf is present in all three determinable m1s.

Two m2s are known, differing from m1 in that the trigonid is subequal in width to the talonid, the anterior cingulid is much longer transversely, a weak preprotocristid connects the anterior cingulid with the protoconid, a metastylid is absent, and a direct hypolophid connection between the entoconid and hypoconid is present on SDSNH 48016.

At least two m3s are known. Both are anteroposteriorly shorter than m1–2. Both lack a preprotocristid, have a much smaller entoconid than in m1–2, and have a trigonid wider than the talonid. An isolated m3 from SDSNH Loc. 3701 (SDSNH 47991) differs from the above m3s in that it is anteroposteriorly longer, has a preprotocristid, and a strong posterior ectolophid. It may or may not pertain to *Pauromys*.

Maxillary.—A single maxillary fragment is available (SDSNH 46502, Fig. 7A). A weak ridge is present at the medial edge of the maxillary. The postero-medial edge of the fragment is probably broken along the palatine-maxillary suture. The antero-medial edge

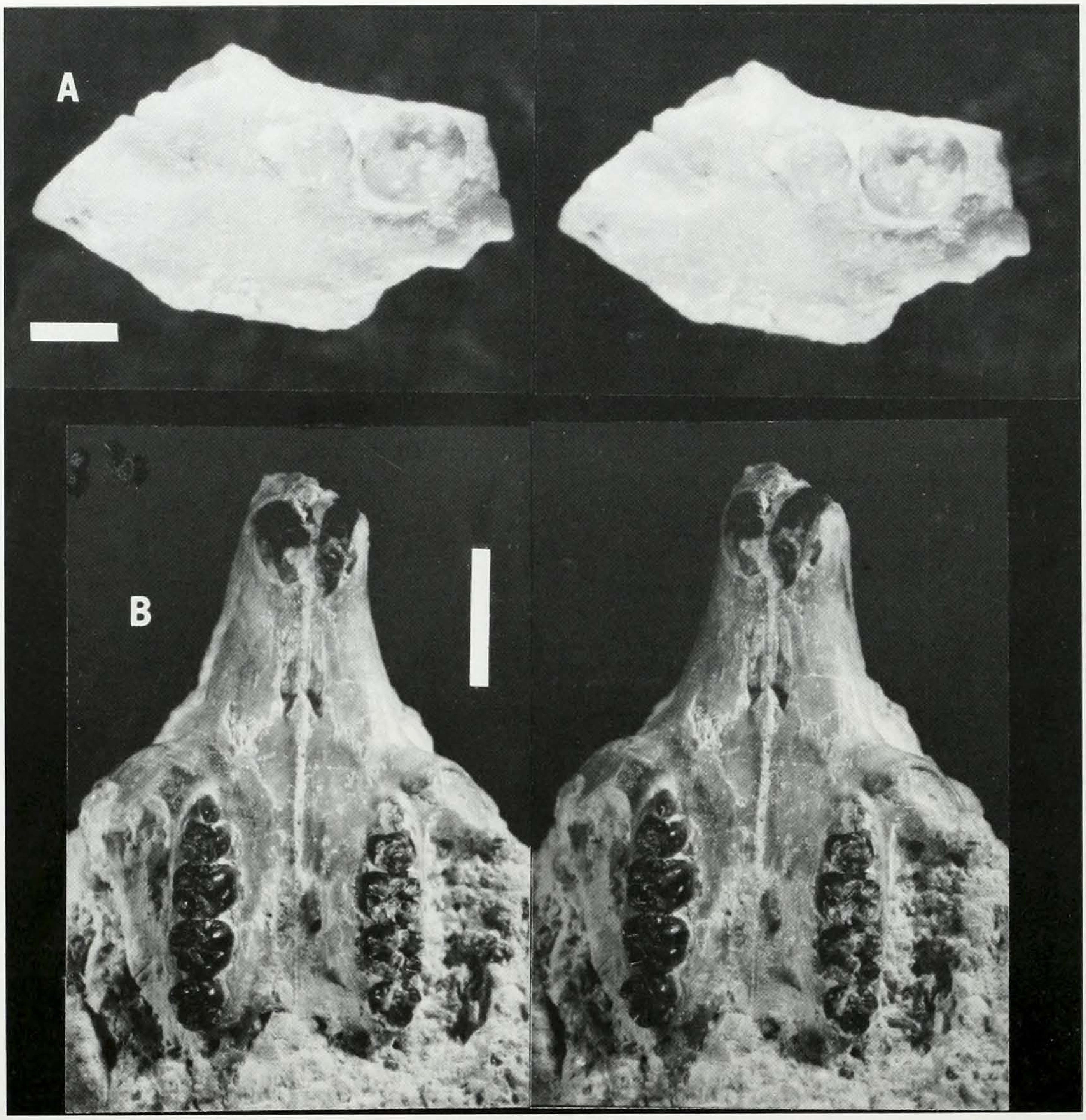


Figure 7. Stereophotographs of (A), SDSNH 46502, L maxilla fragment of *Pauromys lillegraveni* with P4–M1, occlusal view. Scale bar = 1 mm. (B), SDSNH 49210, ventral view of partial skull of *Sciuravus powayensis* showing features of the anterior zygomatic root. Note knob for origin of masseter lateralis superficialis located anterolateral to P3. Scale bar = 5 mm.

of the fragment is apparently broken across the maxillary, and there is no indication of the posterior end of the left incisive foramen. Anterior to P4, a small damaged knob of bone seems to be present in the same relative position as the prominent knob for the attachment of the masseter lateralis superficialis in *Simimys* (see below). A similar knob also seems to be present in the maxilla of *Pauromys* sp. illustrated by Dawson (1968, fig. 41) from Powder Wash. In *Pauromys* the knobs are located more directly anterior to P4 than in *Sciuravus nitidus* (Dawson 1961, plate III) and *S. powayensis* (Fig. 7B). Immediately anteromedial to the damaged bony knob on SDSNH 46502 is a prominent depression in the maxilla, similar in location and orientation to but deeper than that seen in *Sciuravus powayensis*. Not enough of the maxilla is preserved on SDSNH 46502 to reveal whether the anteroventral edge of the inferior zygomatic root was distinctly ridged as in *Sciuravus* and *Pauromys* sp. from Powder Wash. No upper incisors of *Pauromys lillegraveni* have been identified.

Upper Cheek Teeth.—Three P4s are known. Two of them are isolated and unworn, while one is present in a maxilla fragment and somewhat worn (SDSNH 46502). The teeth are three-rooted, with subequal anterolabial and posterolabial roots and a larger lingual root. The anterolabial root juts out from the base of the crown in an anterodorsal direction, as implied for *Pauromys* sp. by Dawson (1968, fig. 41). The crown is anteroposteriorly compressed, oval in occlusal outline, and quite small relative to M1. A distinct anterior cingulum is present on SDSNH 47710 but not on SDSNH 56685. The protocone is roughly conical and is connected to the anterolingual base of the paracone by a distinct preprotocrista. The paracone is subequal to the protocone. A postprotocrista extends posteriad from the protocone apex to merge into the posterior cingulum, which ends at the posterolingual base of the metacone. There is no hypocone. The metacone is slightly compressed anteroposteriorly and slightly larger than the protocone and paracone. SDSNH 47710 has a distinct metaconule fused to the anterolingual base of the metacone, but a metaconule is absent in SDSNH 56685.

M1–2 are best distinguished with reference to SDSNH 46502 (L maxillary fragment with P4–M1; Fig. 7A) and SDSNH 46503 (LM2; not figured). The latter tooth is probably associated with the maxilla, as both were found in the same 30 kg-batch of screen-washed matrix, have similar crown colors, are worn to the same degree, and show a similar dissolution of parts of their labial faces. In general, these teeth are quite similar in crown and root morphology to the M1–2s of *Simimys* described by Lillegraven and Wilson (1975).

Three teeth are identified as M1s. As in *Simimys*, the anterior width is slightly less than the posterior width. SDSNH 46535 is complete and unworn. It has a strong anterior cingulum and no anterocone. The protocone is strong and conical, sending a strong preprotocrista to the anterolingual base of the paracone. There is no protoconule. The paracone is conical and subequal to the protocone. The hypocone is strong, conical, and taller than the protocone. The posthypocrista extends from the hypocone apex to become the posterior cingulum, which then extends to the anterolabial base of the metacone. A centrally located mesocone is connected to the hypocone by a short prehypocrista (posterior mure of some authors). A minute mesostyle is present. The metacone is slightly larger and taller than the paracone.

Two M2s are known; they differ from M1 in being slightly wider anteriorly than posteriorly, and their metacones and hypocones are shorter than their paracones and protocones, respectively. A postprotocrista (anterior mure of some authors) is present in both M2s, connected to the mesocone. In SDSNH 46534, the prehypocrista connects with the lingual base of the metacone.

A single isolated M3 may pertain to *P. lillegraveni* (SDSNH 46536) but it is heavily worn and cannot be confidently distinguished from *Metanoiamys*. Measurements of the cheek teeth of *Pauromys lillegraveni* are given in Table 5.

Discussion.—Walton (1993) noted that the highly reduced p4 in the type specimen of *P. perditus* may be diagnostic of the genus. This condition is also present in *P. lillegraveni*, corroborating the biological reality of this character. Accordingly, the morphological concept of *Pauromys* adopted here is narrower than that used by most recent workers, and I exclude from the genus certain species previously referred to *Pauromys*.

Pauromys schaubi was named by Wood (1959) on the basis of AMNH 11722, a mandible fragment with the roots of p4 and complete m1–2, from the Twin Buttes Member of the Bridger Formation. Wood's (1959, fig. 1) illustration shows that the p4 of "*P.*" *schaubi* must have been substantially larger than that of either *P. perditus* or *P. lillegraveni*, while the m1 trigonid was not as narrow relative to the talonid as in the latter two species. The cheek teeth in AMNH 11722 are also similar in size, proportions, and general morphology to those of *Metanoiamys* and certain species of *Apatosciuravus* and *Knightomys* (e.g., Flanagan 1986, figs. 3–5). Until more complete material is recovered, "*P.*" *schaubi* is here tentatively excluded from *Pauromys*.

Dawson (1968) described a large sample of isolated teeth from the Green River Formation of Utah (early Bridgerian Powder Wash locality). She conservatively assigned the specimens to *Pauromys* sp., and suggested that larger samples from the Bridger Basin might grade morphologically into the Powder Wash sample. Nevertheless, Dawson noted that the available Powder Wash p4s were larger and had better developed trigonids (i.e., were more primitive) than the p4 in the type of *P. perditus*. This situation might constitute a stage-of-evolution argument for a relatively younger age for the poorly constrained type locality of *P. perditus* (Dry Creek). Unfortunately, the latter can be restricted only to Bridger B or C (Dawson 1968:354, Gazin 1976:10).

Nelson (1974) assigned six isolated teeth from the Fowkes Formation of Wyoming (later Bridgerian) to *Pauromys* sp. Although the two molars illustrated by Nelson (1974, fig. 10) are morphologically consistent with this generic assignment, there are no fourth premolars in the sample. Korth (1984) assigned nine isolated teeth from the Wind River Formation of Wyoming (Wasatchian) to *Pauromys* sp. Unlike the situation in undoubted species of *Pauromys*, however, the p4 illustrated by Korth (1984, fig. 29B) is only about 15% shorter than m1. Finally, Flanagan (1986) assigned a single isolated upper molar from the San Jose Formation of New Mexico (Wasatchian) to *Pauromys* sp. More complete material of the species described by Nelson (1974), Korth (1984), and Flanagan (1986) must be collected for their assignment to *Pauromys* to be corroborated.

TABLE 5. Measurements of cheek teeth of *Pauromys lillegraveni*.

	P4		M1			M2			M3		
	AP	W	AP	AW	PW	AP	AW	PW	AP	AW	
SDSNH 47710	0.70	0.71	—	—	—	—	—	—	—	—	
SDSNH 56685	0.69	0.70	—	—	—	—	—	—	—	—	
SDSNH 46502	0.66	0.78	1.17	0.96[a]	0.99[a]	—	—	—	—	—	
SDSNH 46535	—	—	1.22	1.08	1.15	—	—	—	—	—	
SDSNH 48013	—	—	1.18	1.15	1.18	—	—	—	—	—	
SDSNH 46503	—	—	—	—	—	1.17[a]	1.17[a]	1.13	—	—	
SDSNH 46534	—	—	—	—	—	1.25[a]	1.09[a]	1.02[a]	—	—	
SDSNH 46536	—	—	—	—	—	—	—	—	0.97	0.97	
	p4		m1			m2			m3		
	AP	WTAL	AP	WTRI	WTAL	AP	WTRI	WTAL	AP	WTRI	WTAL
SDSNH 47708	0.57	0.53	—	—	—	—	—	—	—	—	—
SDSNH 47709	0.69	0.68	—	—	—	—	—	—	—	—	—
SDSNH 46501	0.55	0.62	1.17	0.90	0.94	1.21	1.05	1.08	1.09	0.97	0.87
SDSNH 46530	—	—	1.17	0.81	0.94	—	—	—	—	—	—
SDSNH 46531	—	—	1.20	0.79	0.92	—	—	—	—	—	—
SDSNH 46532	—	—	1.29	0.79[a]	0.92[a]	—	—	—	—	—	—
SDSNH 48011	—	—	1.18	0.82	0.99	—	—	—	—	—	—
SDSNH 48012	—	—	1.15	0.76	0.90	—	—	—	—	—	—
SDSNH 48016	—	—	—	—	—	1.21	0.97	1.05	—	—	—
SDSNH 46533	—	—	—	—	—	—	—	—	1.09[a]	1.03[a]	0.78[a]

[a] Value a minimum owing to slight damage.

Emry and Korth (1989) named the species *Pauromys exallos* on the basis of eleven isolated teeth from the Sheep Pass Formation of Nevada (Bridgerian). It is uncertain whether this generic assignment is correct. The p4 (USNM 336401; Emry and Korth 1989, fig. 4C) referred to "*P.*" *exallos* is subequal in size to the molars assigned to this species and is relatively much larger than the p4s in *P. perditus* and *P. lillegraveni*. Therefore, if USNM 336401 is in fact conspecific with the other teeth assigned by Emry and Korth to "*P.*" *exallos*, then this species is clearly excludable from *Pauromys*. In my opinion, however, USNM 336401 probably pertains to *Microparamys sambucus* (e.g., compare with the p4 in UCMP 96399 and numerous p4s of *M.* sp. cf. *M. minutus* and *M. woodi* in SDSNH collections). Similarly, an M3 figured by Emry and Korth (1989, fig. 4B; USNM 336429) has the posterior elongation typical of *Microparamys* and is distinctly larger than USNM 417474 and 404695, isolated M3s that are more securely assignable to "*P.*" *exallos*. While it is still possible that "*P.*" *exallos* is a valid species of *Pauromys* possessing greatly reduced but as yet uncollected premolars, this generic assignment has not been confidently established.

Walton (1993) named two new species of *Pauromys* from the Uintan of Texas, *P. texensis* (early and late Uintan) and *P. simplex* (late Uintan). From her figures and some casts, it appears that some specimens of *P. texensis* and *P. simplex* may be referable to genera other than *Pauromys*. For example, TMM 41745-54 and TMM 41745-102 (Walton 1993, figs. 6D–E), are more similar in morphology and relative size to dp4 and p4 of *Metanoiamys agorus* than to p4 of *Pauromys perditus* or *P. lillegraveni*. TMM 41745-145 (Walton 1993, fig. 6A), a probable DP4, closely resembles the DP4 of *Metanoiamys* in its trapezoidal occlusal outline and size relative to the molars. Similarly, TMM 41745-383, identified by Walton (1993, fig. 6O) as an M2? of an indeterminate sciuravid, has the typical quadrate occlusal outline of a P4 of *Metanoiamys*. On the basis of their relatively large size, if the DP4 and dp4 referred by Walton (1993, fig. 8J-K) to *P. simplex* are in fact conspecific with the rest of the hypodigm, then this species is definitely not assignable to *Pauromys*. Similarly, the lower molars and M2 of *P. simplex* illustrated by Walton (1993, figs. 8D, 8G, 8H) are quite similar to those of *Metanoiamys agorus* in size, occlusal outline, and simple construction of the median valley. M. R. Dawson (pers. comm.) also suggests that some of the Texas specimens are referable to an undescribed, relatively advanced sciuravid genus known from the late Uintan of Badwater, Wyoming. As noted by Walton (1993), collection of mandibles and maxillae of the Texas species will be necessary to establish the identity of these teeth confidently.

Pauromys has traditionally been assigned to the Sciuravidae, which is presumably a paraphyletic taxon characterized in part by the primitive retention of two upper premolars. The general morphology of the molars of *Pauromys*, however, is very similar to that seen in *Simimys* and other undoubted Myodonta. The absence of P3 is also a derived character shared with other myomorphs. Thus, I regard *Pauromys* as a primitive member of the Myodonta, slightly more derived than *Armintomys*. Although the zygomasseteric structure of *Pauromys* is unknown, this genus seems likely to have descended from a small-bodied hystricomorphous rodent similar to *Armintomys* but with ungrooved incisors. The presumed hystricomorphy of *Pauromys* is consistent with the position of the anterior end of the masseteric fossa in this genus (below the m1 talonid) being identical to that in the hystricomorphous rodent *Simimys* (see below).

Several authors have commented on the possibility of a close relationship between *Pauromys* and *Simimys* (Wilson 1949, Dawson 1968, Lindsay 1968, Walton 1993). Other workers have proposed that *Simimys* was an immigrant from Asia, without a North American ancestry (Vianey-Liaud 1985). With the discovery of *Pauromys lillegraveni*, the first hypothesis seems more attractive. As discussed above, there are detailed similarities in the mandible, lower incisor, ventral zygomatic root, and molars between the late early Uintan *P. lillegraveni* and the late Uintan *Simimys* sp. in San Diego. The latter genus is known to differ from the former only in its more derived loss of p4, narrower m1 trigonid, reduced P4 (or DP4), and greater diastemal concavity. *Pauromys lillegraveni* possesses no known autapomorphies that exclude its being directly ancestral to *Simimys*.

Superfamily Dipodoidea Weber, 1904

Dipodoidea *incertae sedis*

Simimys (Wilson, 1935a, b)

Type Species.—Simimys simplex (Wilson, 1935a).

Included Species.—Simimys simplex (Wilson, 1935a) and *Simimys landeri* Kelly, 1992.

Distribution.—Known only from the late Uintan and Duchesnean (late middle Eocene) of southern California.

Emended Diagnosis.—Mouse-sized basal dipodoid rodent. Cheek teeth of generalized myodont construction. Zygomasseteric structure hystricomorphous. Derived with respect to *Pauromys* in the reduction of P4 to a single-rooted peg, the loss of p4, and the narrowing of the m1 trigonid. Similar in most respects to *Pappocricetodon*, but with weaker or absent anteroconids and anterocones on m1 and M1 and a separate neurovascular infraorbital canal. Dentally similar to *Elymys*, but with stronger mesolophs and mesolophids and a relatively more anteroposteriorly elongate m1. Primitive with respect to *Plesiosminthus* and later zapodids in having ungrooved upper incisors, having only a moderately concave mandibular diastema, having the ridges that define the masseteric fossa extending anteriorly only to below the m1 talonid, and having the posterior margins of the incisive foramina extending posteriorly only to the level of the bony knob anterior to P4. Possible autapomorphy: Strong knob present on ventral zygoma anterior to P4 for origin of masseter lateralis superficialis.

Discussion.—Simimys is among the most interesting of California Eocene rodents. Its first historical appearance in the region helps characterize the beginning of the late Uintan (Walsh 1996), and it is by far the most abundant micromammal at virtually all well-sampled late Uintan sites. The genus was named by Wilson (1935a, b) on the basis of several lower dentitions from the Sespe Formation in Ventura County. Wilson (1935a) originally recognized two species: *S. simplex* (the type species, from the Duchesnean locality CIT 150), and *S. vetus* (from the late Uintan locality CIT 207). Later, from the late Uintan locality CIT 180, Wilson (1949) named a new species that he questionably assigned to the genus, *S*?. *murinus*. On the basis of the damaged holotype skull of this species (LACM [CIT] 3529), Wilson (1949:19) stated "the area immediately in front of M1 is somewhat damaged, but P4 appears to be absent. If it is present, the root must be very slender indeed."

Lillegraven and Wilson (1975) described a large sample of isolated teeth of *Simimys* from the Santiago Formation of northwestern San Diego County (UCMP Loc. V-72088) and compared it with the original Sespe specimens described by Wilson. They documented extensive morphological variation in the V-72088 sample and observed that it encompassed all of the features previously considered diagnostic of Wilson's three named species. They therefore regarded *S. vetus* and *S. murinus* as junior synonyms of *S. simplex* and assigned all known southern California specimens of the genus to the latter species. Finally, Kelly (1992) named the large species *Simimys landeri* on the basis of isolated teeth from the later Duchesnean Simi Valley Landfill local fauna. This species may also occur in the questionably Duchesnean "Sweetwater" Formation of southwestern San Diego County on the basis of specimens reported by Walsh (1991a) as "Myomorpha, unidentified genus and sp."

As will be discussed in more detail below, different interpretations of the relative significance of "dipodoid hystricomorphy" and

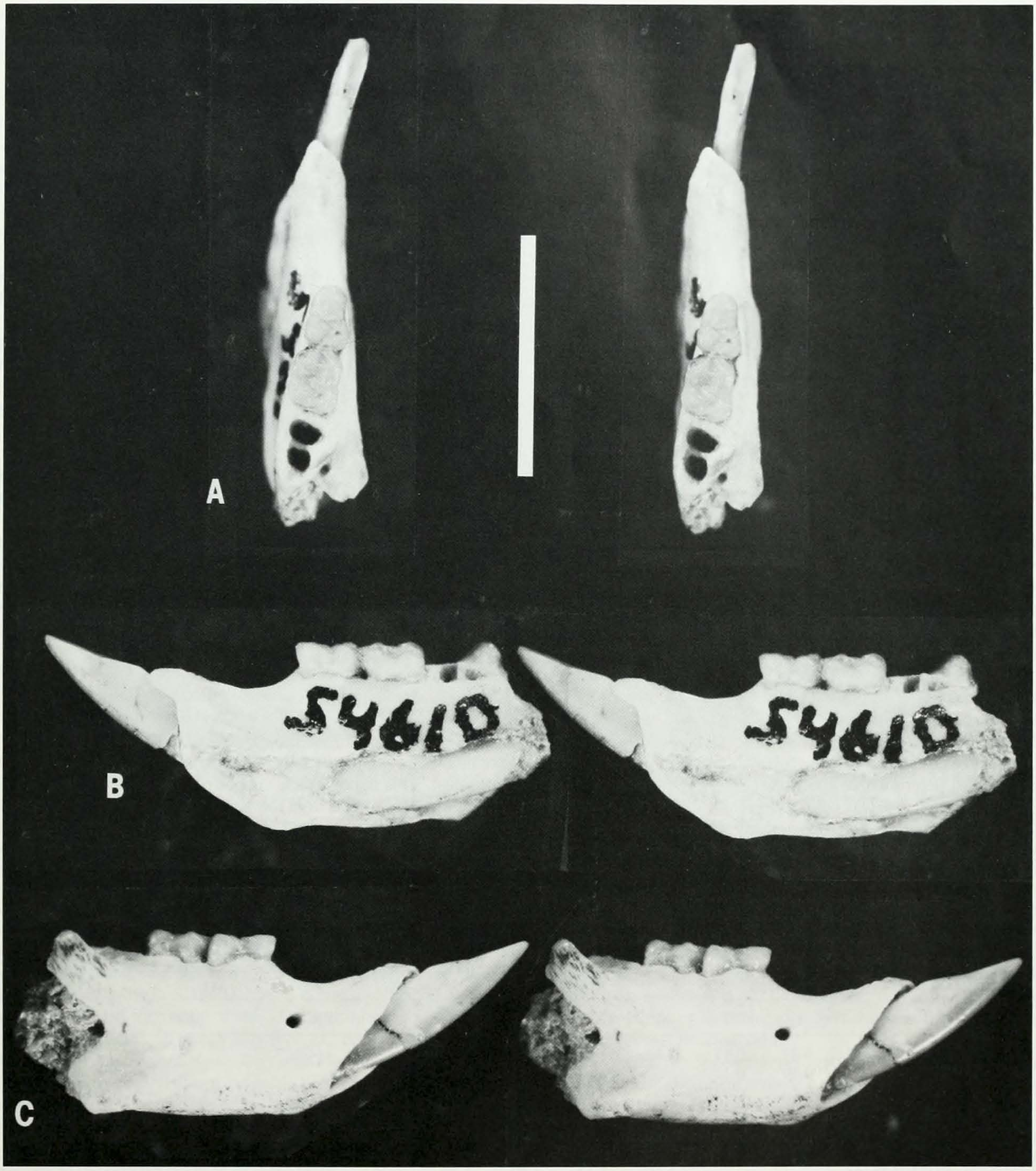


Figure 8. Stereophotographs of SDSNH 54610, R mandible of *Simimys* sp. with i1 + m1-2: (A), occlusal view; (B), medial view; (C), lateral view. Scale bar = 5 mm.

the presumed loss of P4 in *Simimys* have been primarily responsible for the controversy over whether the genus should be regarded as muroid, dipodoid, or neither. The specimens described here shed new light on the possible affinities of this genus.

Simimys sp.
Figs. 8-9

Referred Specimens, Santiago Formation, Member C.—Jeff's Discovery local fauna: SDSNH Loc. 3276: SDSNH 43640, maxilla fragment with M1. SDSNH Loc. 3564: SDSNH 47100, mandible fragment with i1 + m1-2; 47101 and 52224, mandible fragments with m1-2; 47468 and 47807, mandible fragments with m1; 54275 and 56695, maxilla fragments with P4; 47102, maxilla fragment with P4-M1; 49848, maxilla fragment with M1-2; 54116, maxilla fragment with P4 alveolus + M1-2; 54930, maxilla fragment with P4 alveolus + M1-3. An additional 681 isolated teeth are known from SDSNH Locs. 3276 and 3560-3564.

Rancho del Oro local fauna: 53 isolated teeth from SDSNH Locs. 3433, 3436, 3441, 3444, 3449, 3451, 3463, and 3466.

Stadium Conglomerate, Upper Member.—Stonecrest local fauna: 47 isolated teeth from SDSNH Locs. 3530 and 3536.

Mission Valley Formation.—UCMP Loc. V-6893/95866, mandible fragment with damaged m1-3. SDSNH 3870/54610, mandible fragment with i1 + m1-2. SDSNH 4019/60065, mandible fragment with i1 + m2-3. In addition to the specimens studied by Lillegraven and Wilson (1975), about 1597 isolated teeth are known from SDSNH Locs. 3273, 3383, 3426, 3428, 3429, 3539, 3741, and 3822, and hundreds of uncatalogued isolated teeth are known from SDSNH Locs. 3870, 4019, and 4020.

Pomerado Conglomerate, Lower Member.—Eastview local fauna: SDSNH Loc. 3755: SDSNH 56166, maxilla fragment with alveolus for P4 + M1-2. SDSNH 56167, maxilla fragment with alveolus for P4 + M1-3. An additional 55 isolated teeth are known from Locs. 3493 and 3755.

Mandible and Lower Incisor.—See Lillegraven and Wilson (1975) for a detailed description of the molars of *Simimys*. Measurements of cheek teeth in all available mandibular and maxillary specimens of *Simimys* from San Diego County are given in Table 6. Mandibles of *S. simplex* and *S. vetus* were first described from the Sespe Formation by Wilson (1935a); none of these specimens preserves the angle or incisor. Several more complete mandibles are now available from San Diego County (e.g., SDSNH 54610, Fig. 8). The depth of these mandibles below m1 averages 3.35 mm (Table 1). SDSNH 54610 and 60065 are complete enough to show the sciurognathous condition of the angle. As noted by Wilson (1935a), the ridges defining the masseteric fossa converge and terminate anteriorly below the m1 talonid. As seen on SDSNH 47100 and 54610, the dorsal surface of the mandible anterior to m1 is moderately concave, distinctly more so than in *Pauromys lillegraveni*, but not as much as in *Metanoiamys agorus*. A single mental foramen is present on all determinable specimens anterior and ventral to m1, slightly higher than halfway up the lateral side of the mandible. As in *Pauromys*, there is an anteroposteriorly elongated bulge on the medial surface of the mandible below the diastema and m1. On SDSNH 54610, the ascending ramus leaves the dorsal surface of the mandible at the level of the m3 talonid, and, as seen in Fig. 8A, there is a small foramen immediately lateral to the posterior alveolus of m3, as in *Pauromys lillegraveni* and *Plesiosminthus* (Schaub 1930, fig. 9; Wilson 1960:81).

The lower incisor is preserved in several mandibles. The ventral face is distinctly convex, the lateral face is slightly convex, and the medial face is very slightly convex, almost flat. The enamel is ungrooved, extending about one-third of the way onto the lateral face and only a very short distance onto the medial face. A small narrow pulp cavity is present. As noted, the lower incisor of *Simimys* sp. is very similar in proportions and absolute size to that of *Pauromys lillegraveni* (Table 1).

Maxillary and Upper Premolar.—The only specimens to show a significant part of the ventral zygomatic root of the maxillary are SDSNH 56166 and 47102 (Figs. 9A,B), which do not differ in preserved morphology from LACM (CIT) 3529, the holotype skull of *Simimys murinus*. The posterior edge of the ventral zygomatic root lies lateral to P4, as in *Pappocricetodon* (Wang and Dawson 1994). The zygomatic plate is slightly more inclined than in *Pappocricetodon*. As noted by Wilson (1949), there is a prominent knob for the origin of the masseter lateralis superficialis immediately anterior to P4. This structure is well shown in SDSNH 47102, 56166, and 56167. SDSNH 56166 also shows a distinct depression in the maxillary immediately anteromedial to this knob, as also reported for LACM (CIT) 3529 (Wilson 1949:19). The extreme posterior margin of the incisive foramen is preserved on SDSNH 56166 (Fig. 9A), and, as in LACM (CIT) 3529 (Wilson 1949:19), it ends posteriorly at the level of the knob for the origin of the masseter lateralis superficialis, rather than at the level of P4 as in *Plesiosminthus* and other zapodids (Engesser 1979, Korth 1980).

P4 (or DP4) is preserved in place in SDSNH 47102 (Fig. 9B). It is single-rooted, with a tiny peglike crown that is slightly wider than long (Table 6). There are no accessory cuspules or cingula. Given the tiny size of P4 (or DP4) in *Simimys* (Table 6), it is probable that isolated premolars would pass easily through a 30-mesh screen (0.6-mm openings). This hypothesis is supported by the fact that no isolated premolars were picked from the +30-mesh concentrates that resulted from screen-washing about 22,000 kg of matrix from SDSNH Locs. 3273, 3383, and 3564. The only P4/DP4s that were recovered from these sites are still embedded in small pieces of maxillary.

TABLE 6. Measurements of cheek teeth of *Simimys* sp. in maxillary and mandibular fragments.

	P4		M1			M2			M3		
	AP	W	AP	AW	PW	AP	AW	PW	AP	AW	
SDSNH 47102	0.39	0.43	1.29	1.06	1.19	—	—	—	—	—	
SDSNH 54275	0.39	0.44	—	—	—	—	—	—	—	—	
SDSNH 56695	0.40	0.42	—	—	—	—	—	—	—	—	
SDSNH 49848	—	—	1.20	1.01	1.08	1.19	1.07	1.03	—	—	
SDSNH 54116	—	—	1.30	1.09	1.18	1.31	1.21	1.13	—	—	
SDSNH 54930	—	—	1.41	1.20	1.29	1.37	1.30	1.27	0.98	1.02	
SDSNH 56166	—	—	1.40	1.12	1.21	1.39	1.26	1.23	—	—	
SDSNH 56167	—	—	1.29	1.06	1.13	1.31	1.21	1.10	1.08	1.04	
			m1			m2			m3		
			AP	TRI	TAL	AP	TRI	TAL	AP	TRI	TAL
SDSNH 47100			1.26	0.71	0.97	1.32	1.09	1.08	—	—	—
SDSNH 47101			—	—	0.95	1.29	0.93	1.11	—	—	—
SDSNH 47468			1.27	0.69	0.94	—	—	—	—	—	—
SDSNH 47807			1.34	—	1.08	—	—	—	—	—	
SDSNH 52224			1.28	0.68	0.91	—	—	—	—	—	
SDSNH 54610			1.34	—	—	1.34	1.01	1.09	—	—	—
SDSNH 60065			—	—	—	1.39	0.98	1.05	1.26	1.01	0.91

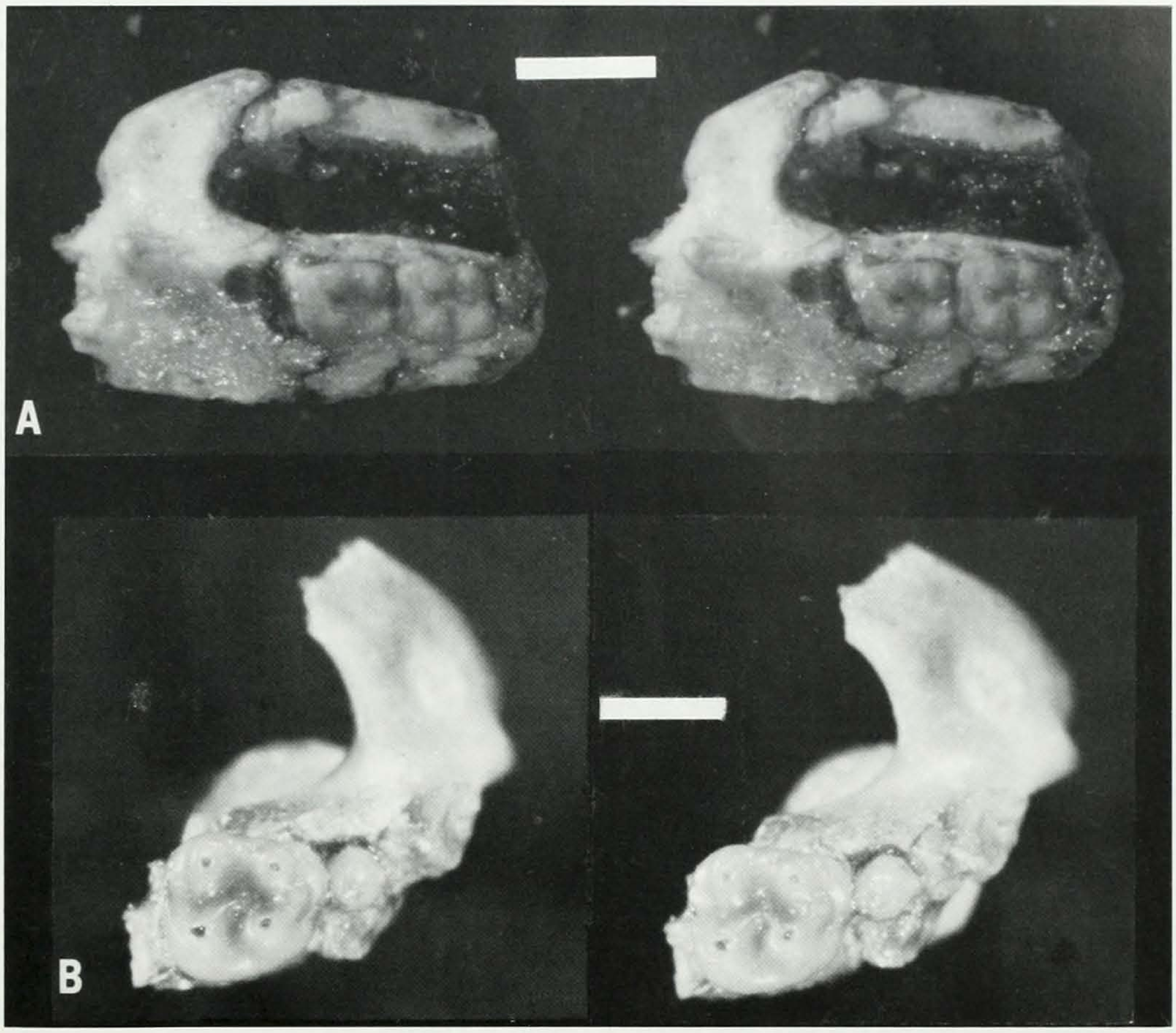


Figure 9. Stereophotographs in occlusal view of (A), SDSNH 56166, L maxillary fragment of *Simimys* sp. with M1–2 and matrix-filled alveolus for P4. Note strong knob anterior to P4 for origin of M. lateralis superficialis. Scale bar = 2 mm. (B), SDSNH 47102, R maxillary fragment of *Simimys* sp. with P4–M1. Scale bar = 1mm.

Frequency of Anterior Appression Facets on M1.—No anterior appression facets were noted on any of the 15 M1s of *Simimys* from the Mission Valley Formation described by Lillegraven and Wilson (1975). However, 18 of 75 determinable M1s from SDSNH Loc. 3273 have small anterior facets (e.g., SDSNH 33000 and 33226), as do 9 of 47 determinable M1s from SDSNH Loc. 3383 (e.g., SDSNH 41561). Such facets are less frequently observed on specimens from the Jeff's Discovery local fauna, in which only 9 of 132 determinable isolated M1s have detectable facets. By analogy with *Metanoiamys agorus* and *Sciuravus powayensis*, it seems probable that most or all San Diego County late Uintan populations of *Simimys* possessed P4 (or DP4) and that the infrequency of anterior appression facets on M1 is caused by the death of some individuals prior to full tooth eruption, and/or slight variations in the relative position of these teeth.

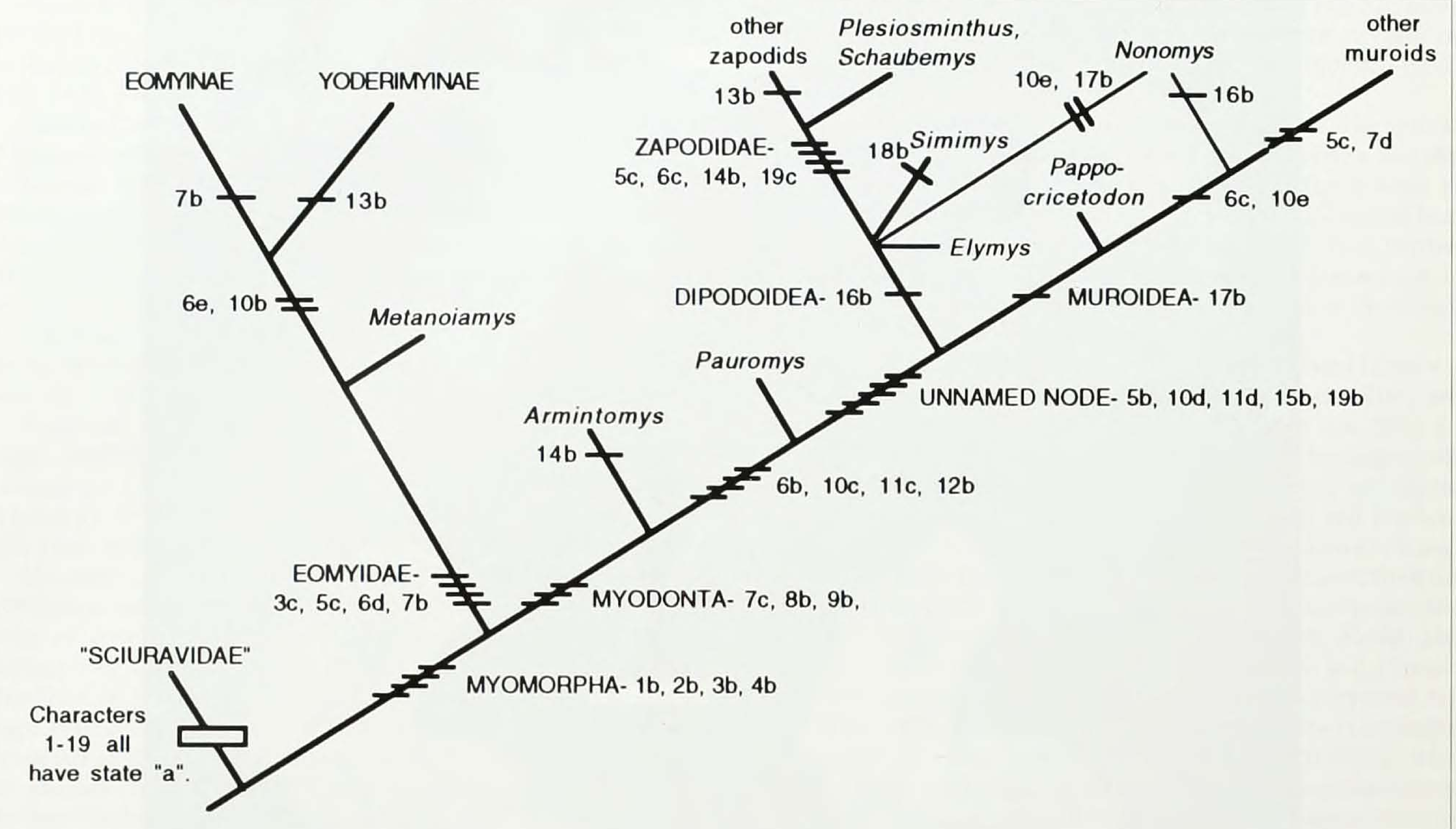
In their examination of at least 100 M1s of *Simimys* from the latest Uintan and/or Duchesnean Camp San Onofre local fauna (UCMP Loc. V-72088), Lillegraven and Wilson (1975) noted a possible anterior wear facet on only one tooth. The apparent rarity of M1 facets from V-72088 may suggest a decreasing frequency of occurrence of P4/DP4 through time. Interestingly, M. R. Dawson (pers. comm.), in studying a large sample of isolated teeth of *Simimys* from the Tapo Canyon and Brea Canyon local faunas of the Sespe Formation, has not identified a single M1 with an anterior appression facet.

It is uncertain whether San Diego County late Uintan populations of *Simimys* (1) possessed and then shed DP4 without replacement, (2) retained DP4 into adulthood, or (3) replaced DP4 with a permanent P4. The first hypothesis would partly explain the infrequency of appression facets on M1, since the absence of a P4 would allow a facet to form only during the brief youth of the animal. This hypothesis is unlikely, however, because several maxillae with moderately to well-worn molars (e.g., SDSNH 47102, 54116, 56167) possess either a premolar or its intact alveolus, showing the presence of a tooth in this locus in adulthood.

Implications for Species-Level Taxonomy.—The new specimens of *Simimys* described here require a conceptual reevaluation of the specific taxonomy of this genus. Potential alternatives are as follows:

1. If all three Sespe populations represented by the holotypes of *S. simplex*, *S. vetus*, and *S. murinus* had in fact retained P4 (or DP4), then the San Diego County specimens would still be assignable to the senior synonym, *S. simplex*.
2. If all three Sespe populations represented by the holotypes of *S. simplex*, *S. vetus*, and *S. murinus* had in fact lost P4/DP4, then the San Diego County specimens could pertain to a new, more primitive species characterized by the retention of P4/DP4.
3. If the Duchesnean *S. simplex* had in fact lost P4/DP4, but the late Uintan populations represented by the holotypes of *S. vetus* and/or *S. murinus* retained P4/DP4, then one of the latter names could be resurrected, and the San Diego County specimens could be assigned to the appropriate Sespe species.

Evaluation of these possibilities must await the collection of



1. M3 length: a. Greater than or equal to M1-2. b. Less than or equal to M1-2.
2. m3 length: a. Greater than or equal to m1-2. b. Less than or equal to m1-2.
3. Incisor enamel: a. Pauciserial. b. Uniserial or trending that way. c. Specialized uniserial.
4. One or more foramina between m3 and ascending ramus: a. Absent. b. Present.
5. Mandibular diastema: a. Essentially horizontal. b. Moderately concave. c. Deeply concave.
6. Masseteric fossa ends below: a. m1-2 contact. b. m1 talonid. c. m1 trigonid. d. p4-m1 contact. e. p4.
7. Zygomasseteric structure: a. Protrogomorphous. b. Sciuromorphous. c. Hystricomorphous. d. Myomorphous.
8. M1-2: a. Essentially square in occlusal outline. b. Slightly AP-elongated.
9. Lower molar mesolophids: a. Weak. b. Variably elongated and progressively complex.
10. P4 : a. 10-15% smaller than M1. b. Subequal to or larger than M1. c. About 50% smaller than M1. d. 1-rooted peg. e. Lost.
11. p4: a. 10-15% smaller than m1. b. Subequal to or larger than m1. c. About 50% smaller than m1. d. Lost.
12. P3: a. Present. b. Lost.
13. Cheek tooth pattern: a. Relatively simple. b. Relatively complex.
14. Upper incisors: a. Ungrooved. b. Grooved.
15. m1 trigonid: a. Slightly narrower than talonid. b. Distinctly narrower than talonid.
16. Separate neurovascular infraorbital foramen: a. Absent. b. Present.
17. Anterocone, anteroconid: a. Absent or weak. b. Moderately to well-developed.
18. Knob for origin of m.l.s.: a. Absent or weak. b. Strong.
19. Posterior ends of incisive foramina located: a. Far anterior to P4. b. Opposite knob for m.l.s. c. Opposite P4.

Figure 10. Cladogram showing hypothesized relationships of various Paleogene myomorph rodents. Geomyoidea and Dipodidae omitted for simplicity. See text for discussion.

more complete maxillae from the Sespe Formation. Until then, I conservatively identify all late Uintan San Diego County specimens of the genus as "*Simimys* sp."

Discussion.—Wilson (1949) noted three characters in which *Simimys* differed from dipodoids: (1) P4 apparently absent, (2) distinct anterior head of masseter lateralis superficialis, and (3) zygomatic plate slightly broadened and inclined. He also noted three characters in which *Simimys* differed from muroids: (1) zygomatic plate essentially horizontal, (2) infraorbital canal not particularly muroid, and (3) absence of a well-developed anterocone or anteroconid. Wilson (1949) concluded that "*Simimys* can perhaps be viewed as a more or less primitive survivor into the late Eocene of a stalk which was ancestral to both cricetids and the Dipodoidea, but in which enough progress had been made in skull structure and dental formula so that it is a muroid rather than a dipodoid rodent."

Largely on basis of the presumed absence of P4, Lindsay (1968) felt that *Simimys* should be regarded as an early cricetid and derived this genus from *Sciuravus* via *Metanoiamys*. Wood (1974) criticized Lindsay's (1968) phylogeny, pointing out that it implied evolution of the zygoma from protrogomorphous to sciuromorphous to hystricomorphous, all in the late [now regarded as middle] Eocene of southern California. Lindsay (1977) acknowledged the difficulties inherent in his previous phylogeny and presented further evidence to support the assignment of *Simimys* to the Cricetidae. Lillegraven and Wilson (1975) felt that assignment of *Simimys* to the Zapodidae (Dipodoidea) was preferable to assignment to the Cricetidae (Muroidea), on the basis of a character apparently unique to the Dipodoidea: presence of separate neurovascular and infraorbital canals (see Emry 1981). Wood (1980) recognized a new monotypic family Simimyidae in order to formalize Wilson's (1949) view on the relationships of *Simimys*. However, Wood assigned the Simimyidae to the Dipodoidea rather than to the ?Muroidea, as proposed by Wilson. Emry (1981) clarified the infraorbital anatomy of *Simimys* as previously discussed by Lillegraven and Wilson (1975) and Lindsay (1977) and assigned the genus to Muroidea, *incertae sedis*, in part on the basis of the presumed loss of P4.

The new material described above clearly shows that at least one late Uintan population of *Simimys* retained P4, and until the Sespe populations can be definitely shown to lack P4, this genus should not be excluded as a potential ancestor of later dipodoid rodents. Whether or not *Simimys* should itself be regarded as a dipodoid is still debatable. Although it had a separate neurovascular foramen as in later dipodoids, it is possible that this is a primitive character that originated relatively early in myodont history, only to be lost by later muroids (the presence of a separate neurovascular foramen in the "dentally muroid" genus *Nonomys* may be consistent with this hypothesis; see below). *Simimys* also has an accessory opening for the mandibular canal between m3 and the ascending ramus, but the presence of this character in *Pauromys* suggests it is primitive for the Myodonta, and cannot be used to allocate taxa to either the Dipodoidea or Muroidea (both the zapodid *Plesiosminthus* and the presumed early cricetid *Pappocricetodon* also have one or more foramina in this area; see below). Unlike later zapodids, *Simimys* retains the primitive condition of having ungrooved upper incisors. In addition, although the posterior margins of the incisive foramina of *Simimys* extend further posteriorly than those of sciuravids, they do not reach the level of P4 as in *Plesiosminthus* and other zapodids. A potential autapomorphy for *Simimys* is the strong knob anterior to P4 for the origin of the masseter lateralis superficialis, which is apparently not comparably developed in any other known Paleogene myomorph or extant dipodoid.

DISCUSSION OF SELECTED PALEOGENE MYOMORPH GENERA

A brief review of selected Paleogene myomorph rodents is presented here to provide perspective on the material of *Metanoiamys*, *Pauromys*, and *Simimys* discussed above, and to highlight pertinent character distributions shown in Fig. 10.

Armintomys.—*Armintomys* was described by Dawson et al. (1990) on the basis of a partial skull from the earliest Bridgerian (late early Eocene) of Wyoming. This genus is hystricomorphous, retains both upper premolars, has slightly anteroposteriorly elongate but otherwise primitive sciuravid-like molars, and lacks a distinct knob for the origin of the masseter lateralis superficialis. Dawson et al. (1990) named the new monotypic family Armintomyidae and questionably assigned it to the Dipodoidea. Wang and Dawson (1994:250) later noted that *Armintomys* lacked the derived neurovascular canal of *Simimys* and later Dipodoidea and suggested it might represent the sister group of dipodoids + cricetids. Although the grooved upper incisor of *Armintomys* is a character shared with *Plesiosminthus* and extant zapodids, given the ungrooved incisors of the more dentally derived myodonts *Pauromys* and *Simimys*, the condition in *Armintomys* is perhaps best assumed to represent a precocious convergence (Fig. 10). The presence in *Armintomys* of an incisor microstructure transitional between pauciserial and uniserial (Dawson et al. 1990) is a potential autapomorphy for either the Myodonta or Myomorpha, and the latter interpretation is favored in Fig. 10.

Elymys.—*Elymys* was named by Emry and Korth (1989) from the Bridgerian of Nevada on the basis of a maxilla fragment with P4–M3 and several isolated teeth. *Elymys* is clearly more derived than *Pauromys* and is similar to *Simimys* in the apparent absence of p4 and the reduction of P4 to a single-rooted peg. Emry and Korth (1989) noted the similarities in molar morphology among *Elymys*, *Plesiosminthus*, and *Simimys* and suggested the possibility of an ancestral relationship between *Elymys* and *Simimys*. This hypothesis represents a different scenario involving a North American origin of *Simimys*, and the discovery of more complete material of *Elymys* is awaited. Critical evidence in this regard will be the presence or absence in *Elymys* of a separate neurovascular canal, a foramen between m3 and the ascending ramus, a distinct knob for the origin of the masseter lateralis superficialis, and the relative positions of the masseteric fossa and incisive foramina.

As shown in Fig. 10, a general trend in myomorphs is the reduction of M3 relative to M1–2. The type specimen of *Elymys*, however, has an M3 that is approximately subequal to M1–2 (Emry and Korth 1989, fig. 5A–C, table 6), which seems anomalous for a myomorph relatively derived dentally. Whether this condition represents individual variation, a retained primitive sciuravid character, or a secondary reenlargement is unclear. If the latter is correct, it could represent an autapomorphy for *Elymys*.

Plesiosminthus and *Schaubemys.*—*Plesiosminthus* is a late Eocene(?) to Miocene zapodid known primarily from Europe and Asia, with one species (*P. clivosus*) currently recognized from North America (Wilson 1960, Korth 1980, Green 1992, Korth 1994). *Schaubemys* is an Oligocene–Miocene North American zapodid (Wilson 1960, Korth 1980, Korth 1994). Strong similarities in dental morphology between *Plesiosminthus* and *Simimys* have been noted by several authors (e.g., Wilson 1949). Mandibles of *Plesiosminthus* described by Schaub (1930, fig. 9) and Galbreath (1953, fig. 26) and mandibles of *Schaubemys* described by Wilson (1960, fig. 131) appear to be similar to those of *Simimys* in their diastemal concavity (more pronounced in *Plesiosminthus* and *Schaubemys*), their possession of an anteroposteriorly elongated bulge on the medial side of the mandible, in the departure of the ascending ramus from the alveolar border at the level of m3, and in their possession of a foramen between m3 and the ascending ramus (the latter condition is variable in *Schaubemys*; see Wilson 1960:84). Known maxillae of *Plesiosminthus* and *Schaubemys* are similar to those of *Simimys* sp. in their possession of a single-rooted peglike P4 (although the crown of this tooth seems to be somewhat more complex in the former two genera). *Plesiosminthus* and *Schaubemys* differ from *Simimys* in that the masseteric fossa extends farther anteriad to below the m1 trigonid (Galbreath 1953:99; Korth 1980, fig. 2), the upper incisors are grooved, there is apparently no distinct knob anterior to P4 for the origin of the masseter lateralis superficialis (Wilson 1960, figs. 126, 128; Green 1977, fig. 3I; Korth 1980, fig. 3A), and the posterior margins of the incisive foramina extend back to the level of P4. Since almost all of the characters in which *Simimys* differs from *Plesiosminthus* and *Schaubemys* appear to be primitive, it seems likely that *Simimys* was close to the line of direct ancestry of the former genera. As noted, the very strong knob anterior to P4 may represent an autapomorphy for *Simimys* that would exclude it from being an actual ancestor of the younger taxa.

Pappocricetodon.—*Pappocricetodon* was named by Tong (1992) to include two species from the late middle Eocene and late Eocene of China. Wang and Dawson (1994) named a third species from the middle Eocene of China, *Pappocricetodon antiquus*, and regarded the genus as the earliest known and most morphologically primitive member of the Cricetidae. *Pappocricetodon antiquus* is similar to *Simimys* sp. in general molar morphology, mandibular structure, and in the possession of a small alveolus for a single-rooted P4 (or DP4). This species also has one or more small foramina between m3 and the ascending ramus (M. R. Dawson, written comm., 1996). *Pappocricetodon antiquus* differs from *Simimys* sp. in its lack of a distinct knob for the origin of the masseter lateralis superficialis, in having stronger anterocones and anteroconids on upper and lower first molars, and most importantly in its lack of a neurovascular infraorbital canal separate from the masseteric infraorbital canal.

The existence of *Pappocricetodon antiquus* in China could be interpreted as evidence favoring the immigration of *Simimys* to North America (e.g., Vianey-Liaud 1985), but the direction of this putative immigration is unclear for two reasons. Although the stronger anterocones and anteroconids in *Pappocricetodon* are probably derived over the condition in *Simimys* (Wang and Dawson 1994), the polarity of the other characters in which the two genera differ is unclear. Second, the precise age of *P. antiquus* relative to *Simimys* is uncertain. Given the $^{40}\mathrm{Ar}/^{39}\mathrm{Ar}$ date of 42.83 ± 0.24 Ma for *Simimys*-bearing strata of the Mission Valley Formation (J. D. Obradovich; Walsh et al. 1996), the first historical appearance of this genus in southern California can probably be constrained to about 43-44 Ma. This date may play a key role in determining whether *Simimys* pre- or postdates the middle Eocene records of *Pappocricetodon antiquus* in China. Unfortunately, the locality of *P. antiquus* is a fissure-filling and cannot yet be assigned a numerical age (M. R. Dawson, pers. comm.).

Nonomys.—The peculiar rodent *Nonomys* was named by Emry and Dawson (1972; 1973) from Chadronian deposits of Wyoming and referred to the Cricetidae (note that the Chadronian NALMA is now regarded as late Eocene; e.g., Prothero and Swisher 1992). Emry (1981) described additional material of *Nonomys* and pointed out that it had a neurovascular canal separate from the masseteric infraorbital canal (as in dipodoids) but also had typical muroid characters such as strong anterocones and anteroconids and lacking P4. Emry (1981) emphasized the dental features of *Nonomys* and placed it in the Muroidea, *incertae sedis*. In contrast, Wang and Dawson (1994) gave more weight to the separate neurovascular canal, assigned *Nonomys* to the Dipodoidea, and regarded it as the sister taxon of *Simimys*. Implicit in the latter decision is the conclusion that the loss of P4 and the development of strong anterocones and anteroconids must have been achieved independently in *Nonomys* and muroids. Given the available evidence, superfamilial assignment of *Nonomys* depends entirely on one's philosophy of character weighting, i.e., can one relatively complex zygomasseteric structure outweigh two dental characters that might be more subject to homoplasy? There is no "correct" answer to this methodological question, and both alternatives to the phylogenetic position of *Nonomys* are shown in Fig. 10. Interestingly, R. J. Emry (pers. comm., 1996) indicates that the two mandibles of *Nonomys simplicidens* figured by Emry (1981, fig. 1) possess a small foramen between m3 and the ascending ramus, as in *Pauromys*, *Simimys*, *Plesiosminthus*, and *Pappocricetodon*.

PROPOSED RELATIONSHIPS OF SELECTED PALEOGENE MYOMORPHA

A generalized hypothesis of cladistic relationships for selected Paleogene myomorphs is shown in Fig. 10, based upon the traditional view that myomorphs were derived from sciuravids [e.g., Jaeger (1988) and Wang and Dawson (1994), but see Vianey-Liaud (1985) and Luckett and Hartenberger (1985) for different scenarios]. The character distributions were obtained from the literature and the new material described above. Polarity determinations and the resulting topology represent my own preferred synthesis of the existing consensus—see especially Wang and Dawson (1994) and Korth (1994)—but no attempt was made to perform a numerical parsimony analysis. Such a study will be more meaningful when better specimens of *Armintomys*, *Pauromys*, *Elymys*, and *Nonomys* are discovered. Note that the Geomyoidea and Dipodidae are excluded from Fig. 10 for simplicity. No attempt is made to place the presumed geomorph *Griphomys* Wilson, 1940b, or the presumed dipodoid *Simiacritomys* Kelly, 1992, on the cladogram, as these two genera are known only from relatively fragmentary material.

The decision as to which nodes certain taxon names should occupy is somewhat arbitrary. Some might prefer to restrict the Myodonta to the most recent common ancestor of the Dipodoidea and Muroidea, and all of its descendants, in which case *Armintomys* and *Pauromys* would not be members of Myodonta. A similar approach would exclude *Simimys* and *Elymys* from the Dipodoidea. See de Queiroz and Gauthier (1990) for a discussion of the logic behind such decisions. A detailed consideration of the semantics of this problem is important, but beyond the scope of this paper.

Character states 1b and 2b (M3/m3 length • M1-2/m1-2 length) together represent a trend in early myomorphs that is clearly derived over the condition in sciuravids and ischyromyids, although exceptions are seen in some taxa, and these characters are unknown in *Armintomys*. Character state 3b (incisor enamel uniserial or trending that way) is assumed to be an autapomorphy for the Myomorpha, based on *Armintomys* (Dawson et al. 1990). The presence of this character should be corroborated in *Pauromys* and *Simimys*. Note that Wahlert (1968), Wahlert and von Koenigwald (1985), and Emry and Korth (1993) reported a derived type of uniserial enamel in *Adjidaumo*, *Paradjidaumo*, *Yoderimys*, and various other eomyids (character state 3c) . It will obviously be important to determine if the same condition exists in the basal eomyid *Metanoiamys*.

Character state 4b (presence of one or more foramina between m3 and the ascending ramus) may be an autapomorphy for the Myomorpha, as it occurs in *Metanoiamys*, *Pauromys*, *Simimys*, *Plesiosminthus*, and *Pappocricetodon* but is absent in *Sciuravus*, *Pareumys*, and ischyromyids. These foramina are also present in at least some extant zapodids (e.g., *Zapus* and *Napaeozapus*) and some (but not all) extant cricetids. The functional significance of these foramina is unknown, and their phylogenetic validity requires further study.

The various derived states of Character 5 (condition of the mandibular diastema) appear to have arisen more than once from the primitive horizontal condition. The earliest known geomorph (*Metanoiamys*) already has a deeply concave diastema. In *Pauromys* it is still virtually horizontal, becomes moderately concave in *Simimys*, *Pappocricetodon*, and *Nonomys*, and independently becomes deeply concave in zapodids and later muroids.

Various states of Character 6 (anterior extent of the masseteric fossa) show much homoplasy. In *Metanoiamys*, the masseteric fossa already reaches as far anteriad as the p4-m1 contact; it reaches to below p4 in all known later eomyids. Anterior advancement of the fossa progressed more slowly in myodonts, since it extends only to below the m1 talonid in *Pauromys*, *Simimys*, and *Pappocricetodon*. Further advancement of the fossa to below the m1 trigonid apparently took place independently in *Plesiosminthus* and later zapodids, and in *Nonomys* and later muroids. Character state 7b (sciuromorphy) is assumed to be an autapomorphy for the Geomorpha with respect to all other myomorphs (e.g., Wahlert 1985), although the zygomasseteric structure of *Metanoiamys* is unknown. Character state 7c (hystricomorphy) is assumed to be an autapomorphy for the Myodonta (Dawson et al. 1990), and is therefore predicted to be present in *Pauromys* and *Elymys*.

The typical "myodont" molar morphology is represented largely by the combination of character states 8b (anteroposteriorly elongated upper molars) and 9b (progressively elongated mesolophids). Characters 10 and 11 (relative size and occurrence of P4 and p4) show two distinct trends. In most sciuravids, P4/p4 is slightly smaller (10-15%) than M1/m1. This primitive condition persists in *Metanoiamys*, but P4/p4 become subequal to or larger than M1/m1 in the

Yoderimyinae and later eomyids (Wood 1974, figs. 29c, 35; Emry and Korth 1993:1047). The opposite trend is seen in myodonts, where P4/p4 are highly reduced in *Pauromys*, P4 is further reduced to a one-rooted peg and p4 is lost in *Simimys* and *Elymys*, and P4 is finally lost in most muroids. P3 is primitively retained in *Metanoiamys* and *Yoderimys*, independently lost in later eomyids and *Pauromys* (character 12).

Character state 16b (separate neurovascular infraorbital foramen present) is assumed to be an autapomorphy for the Dipodoidea (Emry 1981), but, as noted above, its presence in the possible muroid *Nonomys* is problematical (Wang and Dawson 1994 vs. Emry 1981). Two possible phylogenetic positions for *Nonomys* are therefore shown in Fig. 10. In addition, more complete material of *Pauromys* must be collected to demonstrate that a separate neurovascular foramen did not originate even earlier in myodont evolution than shown here.

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LITERATURE CITED

Black, C. C. 1965. Fossil mammals from Montana. Part 2. Rodents from the early Oligocene Pipestone Springs local fauna. Annals of Carnegie Museum 38:1-48.

Chiment, J. J. 1977. A new genus of eomyid rodents from the later Eocene (Uintan) of southern California. Master's thesis, San Diego State University.

Chiment, J. J., and W.W. Korth. 1996. A new genus of eomyid rodent (Mammalia) from the Eocene (Uintan-Duchesnean) of southern California. Journal of Vertebrate Paleontology 16:116-124.

Dawson, M. R. 1961. The skull of *Sciuravus nitidus*, a middle Eocene rodent. Postilla 53.

Dawson, M. R. 1966. Additional late Eocene rodents (Mammalia) from the Uinta Basin, Utah. Annals of Carnegie Museum 38:97-114.

Dawson, M. R. 1968. Middle Eocene rodents (Mammalia) from northeastern Utah. Annals of Carnegie Museum 39:327-370.

Dawson, M. R. 1974. Paleontology and geology of the Badwater Creek area, central Wyoming. Part 8. The rodent *Microparamys* (Mammalia). Annals of Carnegie Museum 45:145-150.

Dawson, M. R. 1977. Late Eocene rodent radiations: North America, Europe, and Asia. Geobios, Mémoire Spécial 1:195-209.

Dawson, M. R., L. Krishtalka, and R. K. Stucky. 1990. Revision of the Wind River faunas, early Eocene of central Wyoming. Part 9. The oldest known hystricomorphous rodent (Mammalia: Rodentia). Annals of Carnegie Museum 59:135-147.

De Queiroz, K., and J. Gauthier. 1990. Phylogeny as a central principle in taxonomy: Phylogenetic definitions of taxon names. Systematic Zoology 39: 307-322.

Emry, R.J. 1981. New material of the Oligocene muroid rodent *Nonomys*, and its bearing on muroid origins. American Museum Novitates 2712.

Emry, R. J., and M. R. Dawson. 1972. A unique cricetid (Rodentia, Mammalia) from the early Oligocene of Natrona County, Wyoming. American Museum Novitates 2508.

Emry, R. J., and M. R. Dawson. 1973. *Nonomys*, new name for the cricetid (Rodentia, Mammalia) genus *Nanomys* Emry and Dawson. Journal of Paleontology 47:1003.

Emry, R. J., and W. W. Korth. 1989. Rodents of the Bridgerian (Middle Eocene) Elderberry Canyon local fauna of eastern Nevada. Smithsonian Contributions to Paleobiology 67.

Emry, R. J., and W. W. Korth. 1993. Evolution in Yoderimyinae (Eomyidae: Rodentia), with new material from the White River Formation (Chadronian) at Flagstaff Rim, Wyoming. Journal of Paleontology 67:1047-1057.

Engesser, B. 1979. Relationships of some insectivores and rodents from the Miocene of North America and Europe. Bulletin of the Carnegie Museum of Natural History 14.

Evanoff, E., P. Robinson, P. C. Murphey, D. G. Kron, D. Engard, and P. Monaco. 1994. An early Uintan fauna from Bridger E. Journal of Vertebrate Paleontology 14, supplement to no. 3:24A.

Flanagan, K. M. 1986. Early Eocene rodents from the San Jose Formation, San Juan Basin, New Mexico. Contributions to Geology, University of Wyoming, Special Paper 3:197-220.

Galbreath, E.C. 1953. A contribution to the Tertiary geology and paleontology of northeastern Colorado. University of Kansas Paleontological Contributions, Vertebrata, 4.

Gazin, C. L. 1976. Mammalian faunal zones of the Bridger middle Eocene. Smithsonian Contributions to Paleobiology 26.

Golz, D. J., and J. A. Lillegraven. 1977. Summary of known occurrences of terrestrial vertebrates from Eocene strata of southern California. University of Wyoming Contributions to Geology 15:43-65.

Green, M. 1977. Neogene Zapodidae (Mammalia: Rodentia) from South Dakota. Journal of Paleontology 51:996-1015.

Green, M. 1992. Comments on North American fossil Zapodidae (Rodentia: Mammalia) with reference to *Megasminthus, Plesiosminthus*, and *Schaubemys*. Occasional Papers of the Museum of Natural History of the University of Kansas 148.

Jaeger, J.-J. 1988. Rodent phylogeny: New data and old problems. Pp. 177-199 *in* M. J. Benton (ed.). The Phylogeny and Classification of the Tetrapods, Volume 2: Mammals. Systematics Association Special Volume no. 35B, Clarendon Press, Oxford, England.

Kelly, T. S. 1990. Biostratigraphy of the Uintan and Duchesnean land mammal assemblages from the middle member of the Sespe Formation, Simi Valley, California. Los Angeles County Natual History Museum Contributions in Science 419.

Kelly, T. S. 1992. New Uintan and Duchesnean (middle and late Eocene) rodents from the Sespe Formation, Simi Valley, California. Bulletin of the Southern California Academy of Sciences 91:97-120.

Kelly, T. S., E. B. Lander, D. P. Whistler, M. A. Roeder, and R. E. Reynolds. 1991. Preliminary report on a paleontologic investigation of the lower and middle members, Sespe Formation, Simi Valley Landfill, Ventura County, California. PaleoBios 13.

Kelly, T. S., and D. P. Whistler. 1994. Additional Uintan and Duchesnean (middle and late Eocene) mammals from the Sespe Formation, Simi Valley, California. Los Angeles County Natural History Museum Contributions in Science 439.

Kennedy, M. P., and G. W. Moore. 1971. Stratigraphic relations of Upper Cretaceous and Eocene formations, San Diego coastal region, California. American Association of Petroleum Geologists Bulletin 55:709-722.

Korth, W. W. 1980. Cricetid and zapodid rodents from the Valentine Formation of Knox County, Nebraska. Annals of Carnegie Museum 49:307-322.

Korth, W. W. 1984. Earliest Tertiary evolution and radiation of rodents in North America. Bulletin of the Carnegie Museum of Natural History 24.

Korth, W.W. 1994. The Tertiary Record of Rodents in North America. Plenum, New York.

Krishtalka, L., R. M. West, C. C. Black, M. R. Dawson, J. J. Flynn, W. D. Turnbull, R. K. Stucky, M. C. McKenna, T. M. Bown, D. J. Golz, and J. A. Lillegraven. 1987. Eocene (Wasatchian through Duchesnean) biochronology of North America. Pp. 77-117 *in* M. O. Woodburne (ed.) Cenozoic Mammals of North America: Geochronology and Biostratigraphy. University of California Press, Berkeley.

Lillegraven, J. A. 1977. Small rodents (Mammalia) from Eocene deposits of San Diego County, California. Bulletin of the American Museum of Natural History 158:221-262.

Lillegraven, J. A., and R. W. Wilson. 1975. Analysis of *Simimys simplex*, an Eocene rodent (?Zapodidae). Journal of Paleontology 49:856-874.

Lindsay, E. H. 1968. Rodents from the Hartman Ranch local fauna, California. PaleoBios 6.

Lindsay, E. H. 1977. *Simimys* and origin of the Cricetidae (Rodentia: Muroidea). Geobios 10:597–623.

Luckett, W. P., and J.-L. Hartenberger. 1985. Evolutionary relationships among rodents: Comments and Conclusions. Pp. 685–711 *in* W. P. Luckett and J. L. Hartenberger (eds.). Evolutionary Relationships Among Rodents: A Multidisciplinary Analysis. NATO Advanced Science Series, ser. A, Life Sciences, Volume 92. Plenum, New York.

Mason, M. A. 1988. Mammalian paleontology and stratigraphy of the early to middle Tertiary Sespe and Titus Canyon formations, southern California. Ph.D. dissertation, University of California, Berkeley.

Nelson, M. E. 1974. Middle Eocene rodents (Mammalia) from southwestern Wyoming. University of Wyoming Contributions to Geology 13:1–10.

Prothero, D. R., and C. C. Swisher, III. 1992. Magnetostratigraphy and geochronology of the terrestrial Eocene–Oligocene transition in North America. Pp. 46–73 *in* D.R. Prothero and W. A. Berggren (eds.). Eocene–Oligocene Climatic and Biotic Evolution. Princeton University Press, Princeton, N.J.

Schaub, S. 1930. Fossile Sicistinae. Eclogae Geologicae Helvetiae 23:616–637.

Schaub, S. 1958. Simplicidentata (= Rodentia). Pp. 659–818 *in* J. Piveteau (ed.). Traité de Paléontologie, Volume 6. Masson, Paris.

Storer, J. E. 1984. Mammals of the Swift Current Creek Local Fauna (Eocene: Uintan, Saskatchewan). Saskatchewan Museum of Natural History Contributions 7.

Storer, J. E. 1987. Dental evolution and radiation of Eocene and early Oligocene Eomyidae (Mammalia, Rodentia) of North America, with new material from the Duchesnean of Saskatchewan. Dakoterra 3:108–117.

Tong, Y.-s. 1992. *Pappocricetodon*, a pre-Oligocene cricetid genus (Rodentia) from central China. Vertebrata PalAsiatica 30:1–16 [in Chinese, English summary].

Troxell, E. L. 1923. *Pauromys perditus*, a small rodent. American Journal of Science, series 5, 5:155–156.

Vianey-Liaud, M. 1985. Possible evolutionary relationships among Eocene and lower Oligocene rodents of Asia, Europe, and North America. Pp. 277–309 *in* W. P. Luckett and J. L. Hartenberger (eds.). Evolutionary Relationships Among Rodents: A Multidisciplinary Analysis. NATO Advanced Science Series, ser. A, Life Sciences, Volume 92. Plenum, New York.

Wahlert, J. H. 1968. Variability of rodent incisor enamel as viewed in thin section, and the microstructure of the enamel in fossil and recent rodent groups. Breviora 309.

Wahlert, J. H. 1978. Cranial foramina and relationships of the Eomyoidea (Rodentia, Geomorpha). Skull and upper teeth of *Kansasimys*. American Museum Novitates 2645.

Wahlert, J. H. 1985. Skull morphology and relationships of geomyoid rodents. American Museum Novitates 2812.

Wahlert, J. H., and W. von Koenigswald. 1985. Specialized enamel in incisors of eomyid rodents. American Museum Novitates 2832.

Walsh, S. L. 1987. Mammalian paleontology of the southern outcrops of the Mission Valley Formation, San Diego County, California. Undergraduate thesis, Department of Geology, San Diego State University.

Walsh, S. L. 1991a. Late Eocene mammals from the Sweetwater Formation, San Diego County, California. Pp. 149–159 *in* P. L. Abbott and J. A. May (eds.). Eocene Geologic History San Diego Region. Pacific Section, Society of Economic Paleontologists and Mineralogists 68.

Walsh, S. L. 1991b. Eocene mammal faunas of San Diego County. Pp. 161–178 *in* P. L. Abbott and J. A. May (eds.). Eocene Geologic History San Diego Region. Pacific Section, Society of Economic Paleontologists and Mineralogists 68.

Walsh, S. L. 1996. Middle Eocene mammal faunas of San Diego County, California. Pp. 75–119 *in* D. R. Prothero and R. J. Emry (eds.). The Terrestrial Eocene–Oligocene Transition in North America. Cambridge University Press, Cambridge, England.

Walsh, S. L., D. R. Prothero, and D. J. Lundquist. 1996. Stratigraphy and paleomagnetism of the middle Eocene Friars Formation and Poway Group in southwestern San Diego County, California. Pp. 120–154 *in* D. R. Prothero and R. J. Emry (eds.). The Terrestrial Eocene–Oligocene Transition in North America. Cambridge University Press, Cambridge, England.

Walton, A. H., 1993. *Pauromys* and other small Sciuravidae (Mammalia: Rodentia) from the middle Eocene of Texas. Journal of Vertebrate Paleontology 13:243–261.

Wang, B.-Y., and M. R. Dawson. 1994. A primitive cricetid (Mammalia: Rodentia) from the Middle Eocene of Jiangsu Province, China. Annals of Carnegie Museum 63:239–256.

Wilson, R. W., 1935a. Cricetine-like rodents from the Sespe Eocene of California. National Academy of Sciences Proceedings 21:26–32.

Wilson, R.W. 1935b. *Simimys*, a new name to replace *Eumysops* Wilson, preoccupied— A correction. National Academy of Sciences Proceedings 21:179–180.

Wilson, R. W. 1940a. Californian paramyid rodents. Carnegie Institution of Washington Publication 514:59–83.

Wilson, R. W. 1940b. Two new Eocene rodents from California. Carnegie Institution of Washington Publication 514:85–95.

Wilson, R. W. 1949. Additional Eocene rodent material from southern California. Carnegie Institution of Washington Publication 584:1–25.

Wilson, R. W. 1960. Early Miocene rodents and insectivores from northeastern Colorado. University of Kansas Paleontological Contributions, Vertebrata, 7.

Wood, A. E. 1937. The mammalian fauna of the White River Oligocene. Part 2. Rodentia. Transactions of the American Philosophical Society 28:155–269.

Wood, A. E. 1959. A new sciuravid rodent of the genus *Pauromys* from the Eocene of Wyoming. American Museum Novitates 1978.

Wood, A. E. 1962. The early Tertiary rodents of the family Paramyidae. American Philosophical Society Transactions (n.s.) 52, part 1.

Wood, A. E. 1974. Early Tertiary vertebrate faunas Vieja Group Trans-Pecos Texas: Rodentia. Texas Memorial Museum Bulletin 21.

Wood, A. E. 1980. The Oligocene rodents of North America. American Philosophical Society Transactions 70, part 5.