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CRICETID RODENTS FROM THE RANCHO EL OCOTE FAUNA, LATE HEMPHILLIAN (PLIOCENE), STATE OF GUANAJUATO

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ABSTRACT

The rodent assemblage of the late Hemphillian El Ocote local fauna in central Mexico resembles that of the Yepómera fauna of northern Mexico, but the El Ocote fauna lacks such northern genera as *Copemys*. Both localities are late Hemphillian in age. A new species of *Prosigmodon* and a new species of *Calomys* are described. El Ocote records the southernmost known occurrence of the primitive woodrat, *Paraneotoma*. There are no South American elements yet known among the rodents, though some of the first ground sloths (*Megalonyx*, *Glossotherium*) in North America are recorded from El Ocote, indicating a "filter bridge" had been initiated between the continents by 4.5 Ma.

Key words: cricetid rodents, Hemphillian, Rancho El Ocote fauna, Guanajuato, Mexico.

RESUMEN

El conjunto de roedores incluidos en el estrato del Henfiliano tardío de la fauna Rancho El Ocote, en el centro de México, se parece al de la fauna de Yepómera, del norte de México, pero en la fauna El Ocote faltan algunos géneros del norte, como por ejemplo *Copemys*. Se describe una especie de *Prosigmodon* y otra de *Calomys*.

La presencia de *Paraneotoma* en El Ocote constituye el registro más austral de este roedor primitivo. No se conoce aún entre los roedores elementos sudamericanos, aunque los primeros registros de *Megalonyx* y *Glossotherium* en América del Norte son referidos al Rancho El Ocote. Su presencia indica el establecimiento de un "puente filtrante" entre los continentes hace 4.5 Ma.

Palabras clave: roedores cricétidos, Henfiliano, fauna local Rancho El Ocote, Guanajuato, México.

INTRODUCTION

The Pliocene terrestrial vertebrate fauna of Mexico is essential to an understanding of the development of the Central American land bridge, continental movements, and late Cenozoic paleoenvironmental conditions. Rancho El Ocote, in central Guanajuato (Figures 1 and 2), is one of the few Pliocene vertebrate localities reported from Mexico and the only one from central Mexico to have received substantial study.

The great American terrestrial fauna interchange occurred with the development of the Central American land bridge near the end of the Pliocene. The age and composition of the El Ocote fauna are particularly significant because it includes *Megalonyx* and *Glossotherium*, ground sloths from South America, but no other vertebrates of obvious South American origin. Such early arrivals from South America suggest an incipient land bridge, allowing "filter" dispersal into North America. An improved record of the fauna and flora of North America and those of South America during this crucial time illuminates important features of the interchange.

PREVIOUS WORK AND GEOLOGICAL SETTING

Fossils from Rancho El Ocote were first brought to light by Arellano (1951), who described three genera of horses and assigned the locality a probable mid-Pliocene age. Mooser, in several publications (1957, 1959, 1963, 1964, 1968, 1973), and Carranza-Castañeda and Ferrusquía-Villafranca (1978, and references therein) studied the horses from El Ocote. Systematic geological and paleontological work at Rancho El Ocote was undertaken by Carranza-Castañeda beginning in 1974, as part of an extensive study by the Instituto de Geología of the Universidad Nacional Autónoma de México (IGUNAM), of the Cenozoic biostratigraphy of Mexico.

At Rancho El Ocote, roughly 100 m of Pliocene floodplain deposits fill a fault-controlled basin surrounded by volcanic highlands. Only the lowest seven or eight meters of exposed section contain Hemphillian fossils of the El Ocote local fauna.

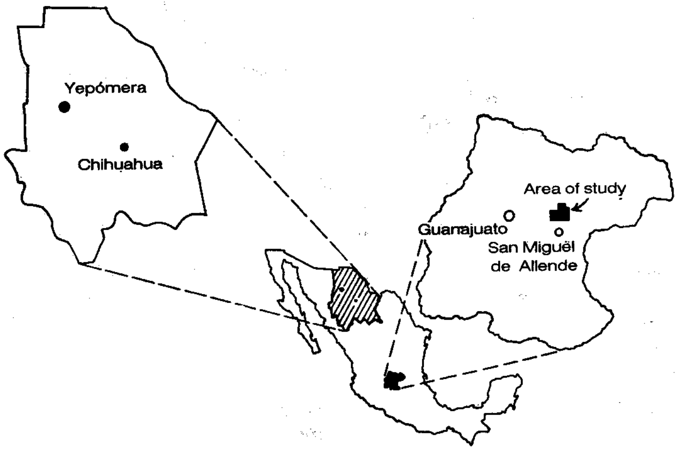

Figure 1.- Index map showing locations Yepómera and Rancho El Ocote.

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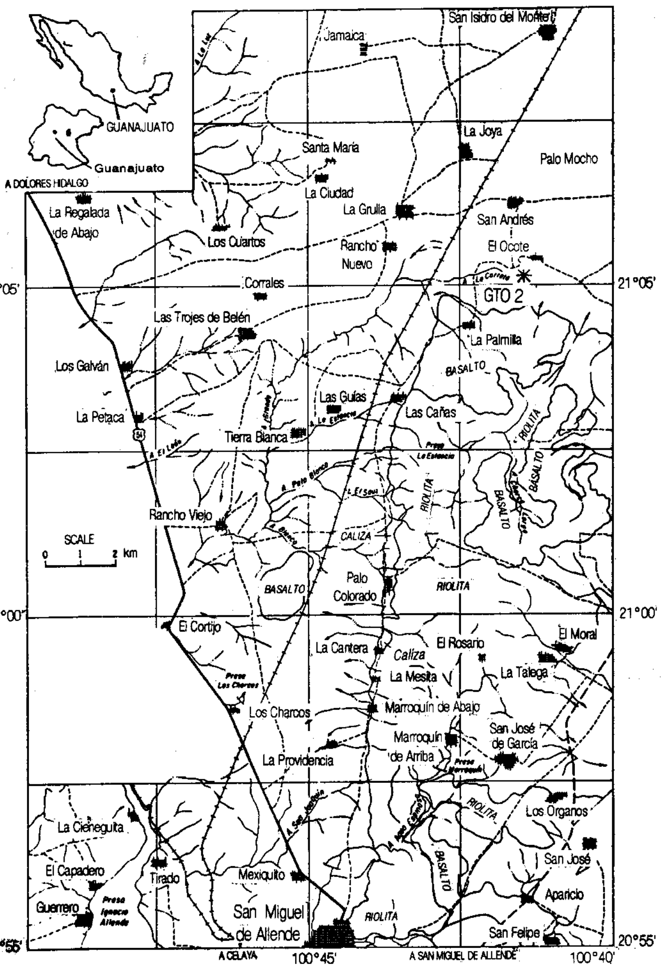


Figure 2.- Location map of the study area, showing locations of Rancho El Ocote (IGUNAM fossil locality GTO 2) and Rancho Viejo.

STRATIGRAPHY

The fossils of El Ocote come from sections GTO 2a, GTO 2b, and GTO 2c, illustrated in Figure 3. Early work in the area was hampered by considerable confusion about the relative ages of stratigraphic units and fossils, which can now be alleviated as a result of careful sampling, observation, and trenching.

Miller and Carranza-Castañeda (1984) recognized several biostratigraphically distinct chronological intervals within the eight meters of exposed Hemphillian section, and determined that the El Ocote fauna extends from the late Hemphillian to the Blancan. The Hemphillian land mammal age was here defined by the presence of *Neohipparion, Astrohippus,* and *Dinohippus*; the Blancan by the occurrence of *Nanippus peninsulatus* with *Equus (Dolichohippus) simplicidens.* This would correspond to an age of roughly 5–2 Ma, by comparison with dated North American faunas. A volcanic ash from the upper (latest Hemphillian) part of the section has produced a date of 4.6 Ma (Kowallis *et al.*, 1986).

The Hemphillian section as a whole is characterized by clay and mud units incised by sand or gravel channels. The lower (late Hemphillian) and upper (latest Hemphillian) units (Carranza-Castañeda, 1989) are distinguished by lithology and different styles of weathering. Section GTO 2b is the most representative, because the units are well exposed and because of the diversity and abundance of the fauna.

The lower unit, 2–4 m thick, is made up of green swelling clay. Pockets of gravel lag consist of subangular to rounded rhyolite and basalt clasts of 3–6 cm (maximum 10 cm) diameter. The basal clay of GTO 2b produces the most diverse and abundant large mammal fauna; this is largely because it has been freshly exposed by trenching, so that the fossils have not been fragmented by the weathering of swelling clays. A fossil-bearing sand and gravel zone (probably a local channel) within the lower unit has been exposed by trenching at GTO 2c, and the South American immigrant *Megalonyx* was recovered from this layer.

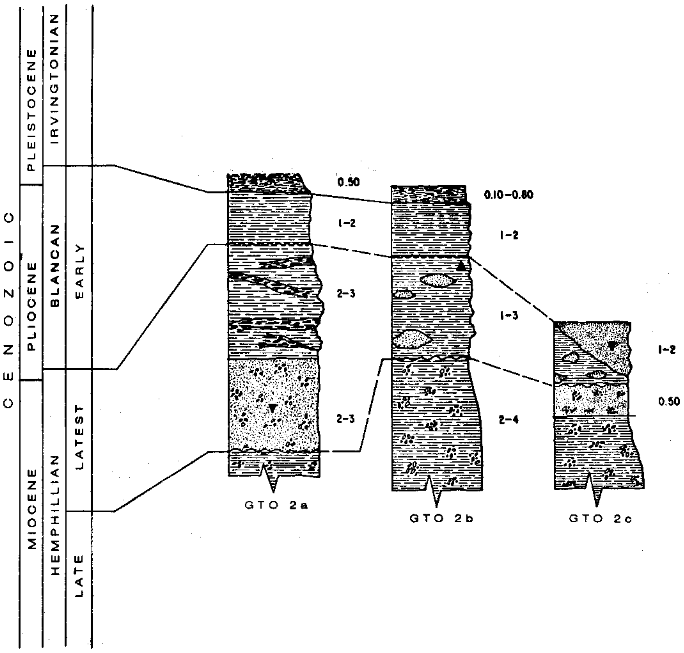


Figure 3.- Stratigraphic sections from Rancho El Ocote and biostratigraphic correlation. Triangles mark sources of microfaunas. Thickness in meters.

The upper (latest Hemphillian) unit, 2–3 m thick, lies disconformably on the lower unit. The upper unit is composed of gray and white volcanic ash and clay. Crossbedded sand occurs in rare, poorly defined lenses. In section GTO 2a, this unit is fine-grained muddy sand and tuff, with quartz-rich lenses. Fossils are generally well-preserved and abundant; mainly isolated teeth and small bone elements of large mammals are recovered, while fish and turtle remains occur with other small vertebrates, such as rodents and rabbits. The rodents which are the subject of this paper came from two different sections within this upper unit (at GTO 2a and GTO 2b). The upper unit at GTO 2c is incised by a sand-mud channel with angular quartz grains; the section above this unit was destroyed by excavation. Elsewhere (GTO 2a) the upper part of the upper unit is channeled, muddy clay, not highly fossiliferous, and is topped by an unconformity (Figure 3). The other South American immigrant, *Glossotherium*, was recovered from this layer in the section GTO 2b.

VERTEBRATE BIOSTRATIGRAPHY

The only other well-studied Hemphillian fauna in Mexico is from Yepómera, in the State of Chihuahua (Figure 1), slightly below 30° latitude. There is a strong resemblance between the faunas of Yepómera and El Ocote (Table 1), but there are no South American elements yet known from Yepómera.

Table 1.- Terrestrial vertebrate fauna reported from Miocene-Pliocene deposits in central and northwestern Mexico.

Faunal list	Rancho El Ocote[1]		Yepómera[2]
	Late He.	Latest He.	
Insectivora			
Notiosorex repenningi			X
Soricidae, indet			X
Edentata			
Megalonyx sp.	X		
cf. *Glossotherium*		X	
Chiroptera			
Plionycterus		X	X
Lagomorpha			
Notolagus velox		X	X
Hypolagus		?	
Rodentia			
Paenemarmota ?barbouri		X	X
Spermophilus sp.			X
Perognathus sp.			X
Perognathus cf. *P. henryredfieldi*			X
Prodipodomys idahoensis			X
Pliogeomys carranzai			X
Copemys near *C. valensis*			X
Calomys elachys		X	X
Calomys baskini		X	X
Calomys winklerorum n. sp.		X	?
Baiomys kolbi		X	X
Prosigmodon chihuahuensis		X	X
Prosigmodon oroscoi		X	X
Prosigmodon ferrusquiai n. sp.		X	
Neotoma (Paraneotoma) cf. *sawrockensis*		X	
Neotoma (Paraneotoma) sp. indet.		X	
Cricetid gen. et sp. indet.		X	
Carnivora			
canid (?coyote)			X
Vulpes			X
Osteoborus	X		?
Agriotherium	X		X
Taxidea mexicana			X
Pseudaelurus	X		X
Machairodus sp.	X		X
Proboscidea			
cf. *Stegomastodon*			X
Stegomastodon sp.	X	X	
Rhynchotherium sp.	X	X	
Perissodactyla			
Neohipparion eurystyle	X		X
Nannippus minor	X		X
Astrohippus stocki	X	X	X
Dinohippus mexicanus	X	X	X
Teleoceras fossiger	X		X
Artiodactyla			
Hemiauchenia	X	X	X
Megatylopus matthewi	X	X	?
Hemiauchenia sp. (small)	X		X
Hexabelomeryx fricki	X		X
Platygonus sp.		?	
Prosthennops	X		X

[1] This study
[2] From Lindsay, 1984; Lindsay and Jacobs, 1985

The Yepómera fauna is late Hemphillian based on the joint occurrence of *Pliogeomys, Agriotherium, Pseudaelurus, Machairodus, Stegomastodon, Astrohippus, Dinohippus, Neohipparion, Teleoceras, and Prosthenops* (Lindsay, 1984). Paleomagnetic studies suggest an age of 4.4–4.5 Ma by the correlation of Lindsay, Opdyke, and Johnson (1984), or ~ 4.8 Ma by the correlation of Repenning and May (1986), in close agreement with the 4.6 Ma isotope date from the upper unit at El Ocote. According to Lindsay and coworkers (1984), either Yepómera or the El Ocote upper beds include the youngest known Hemphillian fauna in North America.

The South American element in the faunas of Guanajuato is established by Blancan time. The Rancho Viejo fauna (Carranza-Castañeda *et al.*, 1981; Miller and Carranza-Castañeda, 1982, 1984), from near Rancho El Ocote (Figure 2), yields *Glossotherium* and the earliest known immigrant rodent from South America—the capybara *Neochoerus* (Carranza-Castañeda and Miller, 1988; Carranza-Castañeda *et al.*, 1981).

Table 1 is a faunal list for El Ocote, showing the differences between the lower (late Hemphillian) and the upper (latest Hemphillian) units, with a list for the Yepómera fauna for comparison. In addition to Pisces, Amphibia, Reptilia, and Aves (not listed), there are thirty-three genera of mammals presently known from El Ocote.

The late Hemphillian was a time of abundance and diversity among tayassuids and equids (Dalquest and Mooser, 1980), and leporid rabbits (Miller and Carranza-Castañeda, 1982). Rodents, particularly the cricetines, were highly diverse, the result of an apparently rapid Hemphillian radiation. By the late Hemphillian, immigration and *in situ* evolution among the cricetines had produced all the modern tribes of North American cricetines (Jacobs and Lindsay, 1984). Later in the Pliocene, members of the Tribe Sigmodontini crossed the Central American land bridge into South America and there underwent an explosive radiation (Baskin, 1986, and references therein).

PALEOECOLOGY

The climate of central Mexico is believed to have been humid and warm throughout the Pliocene (Miller and Carranza-Castañeda, 1984). In contrast, steppe and grasslands prevailed on the High Plains during the late Hemphillian, perhaps corresponding with the end of the Messinian event. Aridity did not arrive to Mexico until later in the Pliocene—evidenced by caliche development in the late Blancan part of the El Ocote section (Ferrusquía-Villafranca and Carranza-Castañeda, 1981). A warm, humid savannah setting is implied by the composition of the Hemphillian macrofauna, including such forms as the semi-aquatic *Teleoceras* (Miller and Carranza-Castañeda, 1984). The diatoms in the section support this conclusion (Rushforth, *in* Miller and Carranza-Castañeda, 1982). It is probable that El Ocote, like Yepómera, represents a more complex environment than a single habitat (Miller and Carranza-Castañeda, 1982).

METHOD

Cusp terminology used in this paper follows that of Lindsay (1972) and is illustrated in Figure 4.

The material was obtained by screenwashing, was undertaken by R. Slaughter in cooperation with IGUNAM. The material discussed in this paper comes from the same stratigraphic unit in two different sections (Figure 3), GTO 2a and GTO 2b. Only a preliminary sample from GTO 2b is presently available. Screen

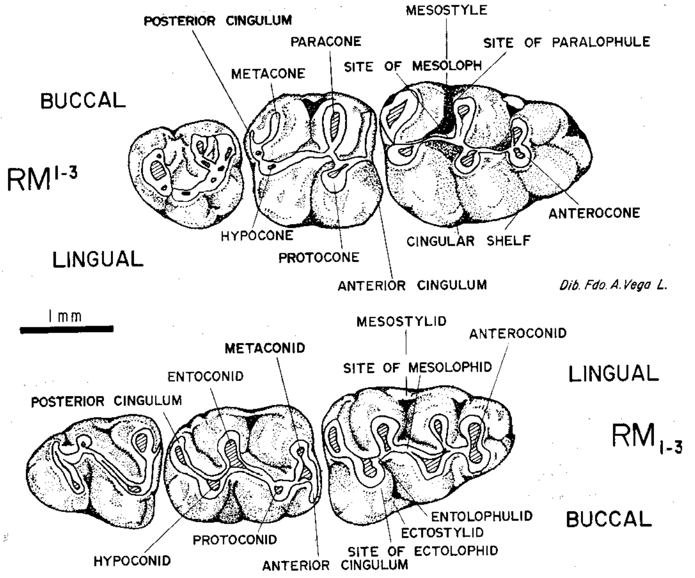


Figure 4.- Composite tooth row for *Prosigmodon ferrusquiai* n. sp. cusp terminology used for all cricetid taxa. Anterior to right. RM^1: IGCU 7254, type. RM^2: 7306. RM^3: 7354. RM$_1$: 7228. RM$_2$: 7342. LM$_3$ (reversed): 7373.

with an aperture of 1 mm was used, consequently the smaller teeth for several taxa were not recovered (Figure 5).

The material used for comparison was obtained from the following institutions:

- IGCU—Instituto de Geología, Ciudad Universitaria
- MNA—Museum of Northern Arizona
- TMM—Texas Memorial Museum
- UALP—University of Arizona Laboratory of Paleontology
- UMMP—University of Michigan Museum of Paleontology
- USGS—United States Geological Survey

SYSTEMATIC PALEONTOLOGY

Order Rodentia
Family Cricetidae
Tribe Hesperomyini
Calomys (Bensonomys)

The history of this genus has been discussed by Baskin (1978, 1986) and by Lindsay and Jacobs (1985). *Bensonomys* is here considered an early subgenus of *Calomys*, the modern vesper mouse of South America, as suggested by Baskin (1978).

Calomys (Bensonomys) baskini Lindsay and Jacobs, 1985
(Plate 1, A-I)

Type specimen—IGCU 1224, right M$_1$, from the Concha fauna, IGCU locality CH-13 (UALP Y35), Chihuahua.

Referred material—Seven isolated cheek teeth. From GTO 2a: two M^{1}s (IGCU 7246, 7265); two M^{2}s (7169, 7307); three M$_1$s (7209, 7212, 7263); one M$_2$ (7379); and two M$_3$s (7151, 7152). From GTO 2b: two M^{2}s (7296, 7309) and one M$_2$ (7330).

Range—IGCU localities CH-11 (UALP Y3), CH-12 (Y30), CH-13 (Y35), and CH-15 (Y39), Yepómera and Concha faunas, Chihuahua. IGCU sections GTO 2a and GTO 2b, El Ocote fauna, Guanajuato. Late Hemphillian, early Blancan.

Diagnosis—As in Lindsay and Jacobs, 1985.

Amended description—When Lindsay and Jacobs (1985) described this species from the Yepómera and Concha faunas, no M^{2}s had been found. The El Ocote fauna provides the first M^{2}s for *C. baskini*.

M^2: The occlusal outline is a rounded trapezoid, longer than it is wide, with a greater anterior width than posterior. Four cusps (paracone, protocone, metacone, and hypocone) are subequal in size, with labial cusps slightly posterior relative to wider lingual cusps. The anterior cingulum is robust and bears a cuspule at the midline, anterior to the protocone. The posterior cingulum is poorly developed and short, in unworn specimens appearing as a cuspule off the metalophule from the hypocone. Two out of four M^2 specimens showed a very small mesoloph (Plate 1, B, E). A cingular shelf develops in the valleys between the paracone-protocone and hypocone-metacone (between the anterior and posterior halves of the tooth), and frequently bears small styles, especially on the lingual side (Plate 1, B, D). There are three robust roots; no preserved rootlets.

MEASUREMENTS (in mm)

		N	X	Range
M^1	length	2	1.90	1.88–1.92
	posterior width	2	1.28	1.16–1.40
M^2	length	4	1.41	1.38–1.42
	anterior width	4	1.22	1.20–1.24
M^3	length	3	1.03	1.02–1.04
	anterior width	3	1.01	0.96–1.03
M$_1$	length	3	1.83	1.68–1.92
	posterior width	3	0.93	0.92–0.96
M$_2$	length	2	1.39	1.38–1.40
	anterior width	2	1.20	1.14–1.26

Remarks—The M^{1}s from both Yepómera and El Ocote usually have a short spur extending from the posterior base of the paracone—a paralophule, in the terminology of Hershkovitz (1962); this feature is often paralleled by a spur at the posterior margin of the tooth formed by the posterior cingulum. The presence of this paralophule helps to distinguish *C. baskini* from other species of *Calomys*. The shape and strongly bilobed anterocone distinguish *C. baskini* from *Prosigmodon oroscoi*.

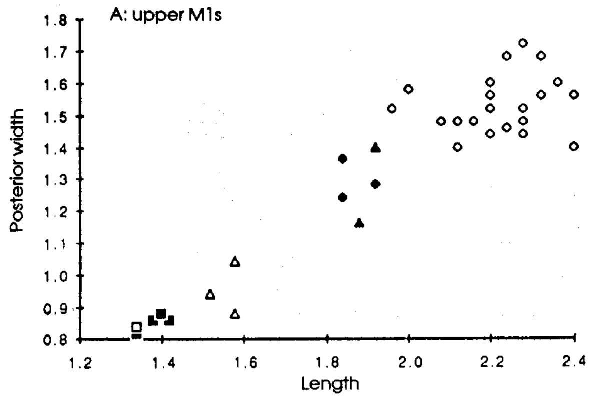
The bilobed anteroconid on M$_1$s from El Ocote is not as pronounced as on those from Yepómera, consequently the anteroconid is not as wide. A small entolophulid emerges from the anterior side of the entoconid in the type specimen from the Concha fauna, but does not appear on any of the El Ocote specimens.

The El Ocote material provides M^{2}s for *C. baskini*, which are absent from the material from Chihuahua. M^{2}s are close in size to *Prosigmodon oroscoi*; the two can be distinguished by the proportion of anterior width to posterior width, which is wider in *Calomys* (hence a trapezoidal occlusal outline) but subequal in *Prosigmodon*. The upper and lower third molars of *C. baskini* are also easily confused with those of *P. oroscoi*, but can be distinguished by the deep valleys in the former and a tendency towards a flattened anterior margin in the latter. M$_3$s are relatively reduced compared to other teeth (Figure 5, C, F); M$_3$ in *C. baskini* is longer for its width but close in size, to the M$_3$ of *Calomys* sp. indet. (IGCU 1192) figured by Lindsay and Jacobs (1985) from the Concha fauna.

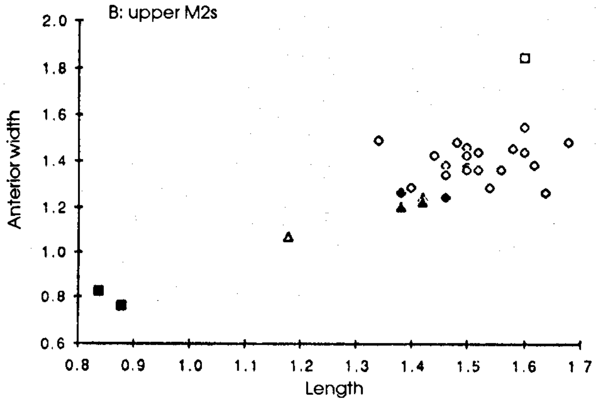
Calomys (Bensonomys) winklerorum n. sp., near *Calomys* sp. indet. Lindsay and Jacobs, 1985
(Plate 1, J–P)

Type specimen—IGCU 7278, an isolated, moderately-worn left M^1 from El Ocote, Guanajuato.

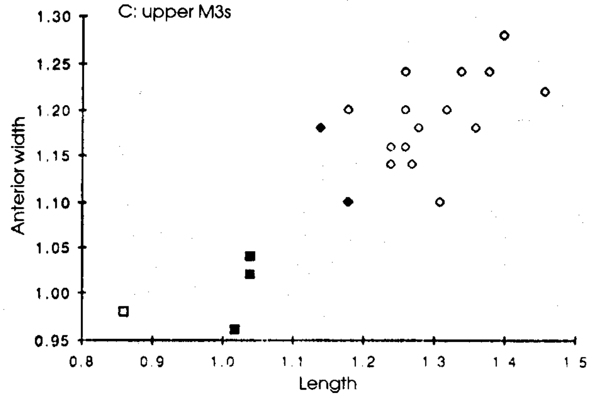
Hypodigm—Seven isolated molars. From GTO 2a: one M^1 (IGCU 7279); one M^2 (7308); one M^3 (7377); and three M$_1$s (7266,



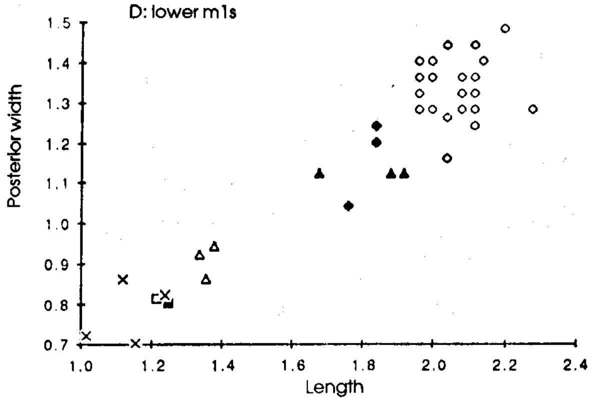
white diamonds: *Prosigmodon ferrusquiai* n. sp.
black diamonds: *Prosigmodon oroscoi*
black triangles: *Calomys baskini*
white triangles: *Calomys winklerorum* n. sp.
black squares*: Calomys elachys* and *Baiomys kolby*
white square: Cricetidae gen. et sp. indet.



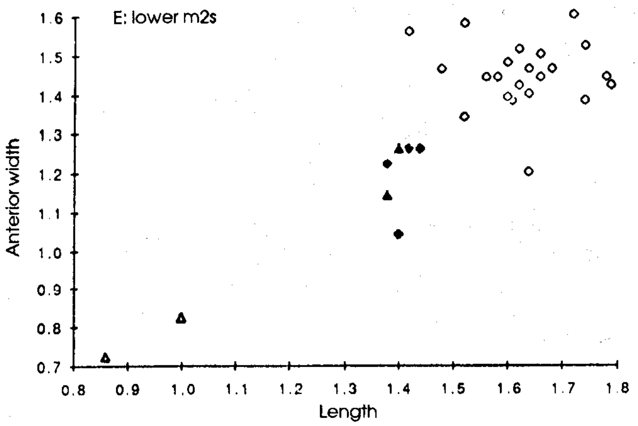
white square: *Prosigmodon chihuahuensis*
white diamonds: *Prosigmodon ferrusquiai* n. sp.
black diamonds: *Prosigmodon oroscoi*
black triangles: *Calomys baskini*
white triangle: *Calomys winklerorum* n. sp.
black squares: *Calomys elachys* and/or *Baiomys kolbi*



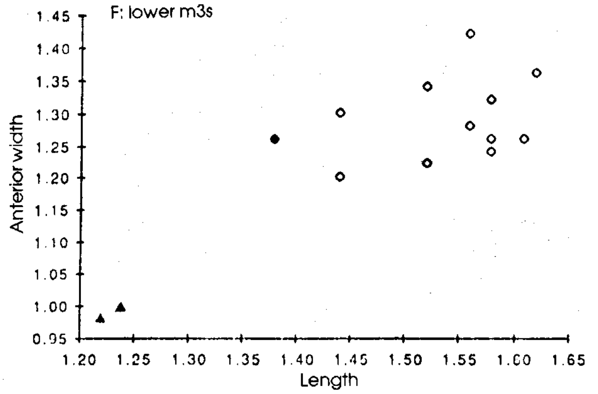
white diamonds: *Prosigmodon ferrusquiai* n. sp.
black diamonds: *Prosigmodon oroscoi*
black squares: *Calomys baskini*
white square: *Calomys winklerorum*



white diamonds: *Prosigmodon ferrusquiai* n. sp.
black diamonds: *Prosigmodon oroscoi*
black triangles: *Calomys baskini*
white triangles: *Calomys winklerorum* n. sp.
Ms: *Baiomys kolbi* and/or *Calomys elachys*
squares: mean measurements on *Baiomys kolbi* and *Calomys elachys* from Yepómera (Lindsay and Jacobs, 1985)

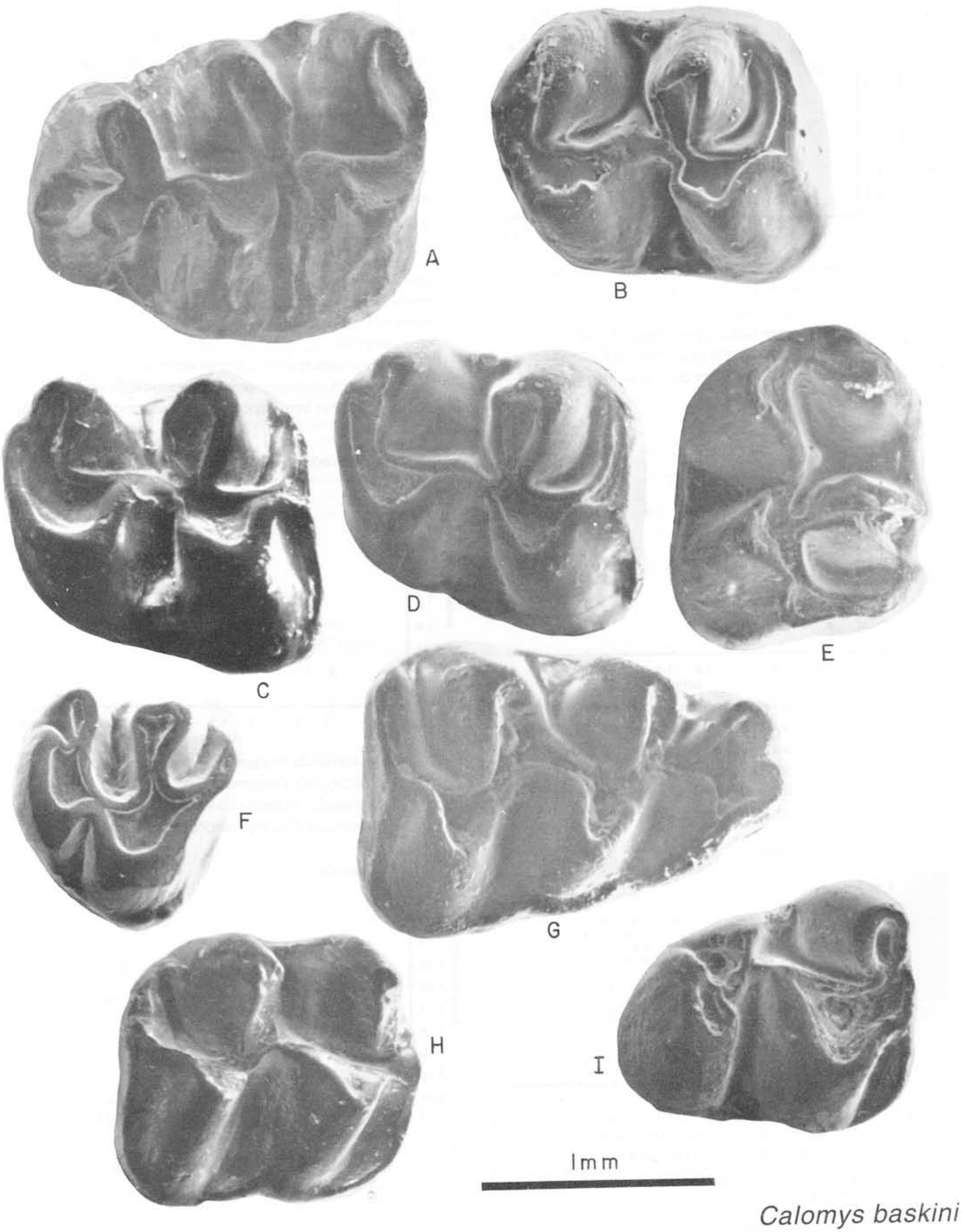


white diamonds: *Prosigmodon ferrusquiai* n. sp.
black diamonds: *Prosigmodon oroscoi*
black triangles: *Calomys baskini*
white triangles: *Calomys elachys* and/or *Baiomys kolbi*



white diamonds: *Prosigmodon ferrusquiai* n. sp.
black diamond: *Prosigmodon oroscoi*
black triangles: *Calomys baskini*

Figure 5.- Scatter plots for tooth measurements on phyllotine cricetids from El Ocote. All measurements in millimeters.



Calomys baskini

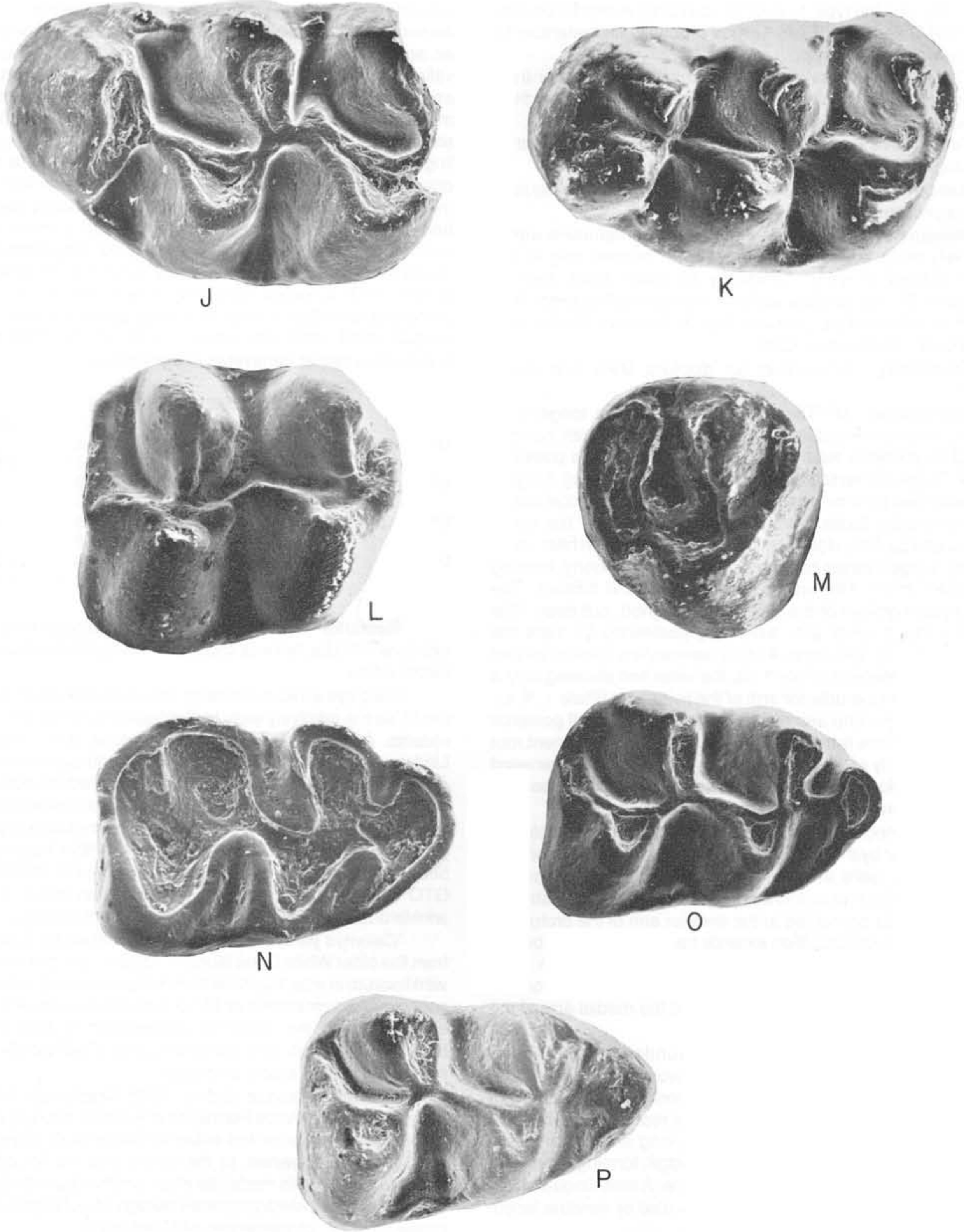


Plate 1.- Orientation as in Figure 4. All to same scale. A—*Calomys baskini*, IGCU 7265, left M^1; B—*Calomys baskini*, IGCU 7169, right M^2; C—*Calomys baskini*, IGCU 7296, right M^2; D—*Calomys baskini*, IGCU 7307, right M^2; E—*Calomys baskini*, IGCU 7309, right M^2; F—*Calomys baskini*, IGCU 7376, right M^3; G—*Calomys baskini*, IGCU 7212, right M$_1$; H—*Calomys baskini*; IGCU 7379, left M$_2$; I—*Calomys baskini*, IGCU 7151, right M$_3$; J—*Calomys winklerorum* n. sp., type, IGCU 7278, left M^1; K—*Calomys baskini*, IGCU 7277, left M^1; L—*Calomys baskini*, IGCU 7308, left M^2; M—*Calomys baskini*, IGCU 7377, right M^3; N—*Calomys baskini*, IGCU 7266, right M$_1$; O—*Calomys baskini*, IGCU 7269, right M$_1$; P—*Calomys baskini*, IGCU 7270, right M$_1$.

7269, 7270); and the type, from GTO 2b (7278). A slightly smaller M^1 from GTO 2a (7277, Plate 1, K) is probably also referable to *Calomys winklerorum* n. sp.

The eight teeth assigned to this species are smaller than the *Calomys baskini/Prosigmodon oroscoi* cluster, but larger than the *Calomys elachys/Baiomys kolbi* cluster (Figure 5, A–D).

Teeth with this size relationship are similar to each other morphologically and probably represent a single species.

Range—GTO 2a and GTO 2b, El Ocote fauna, Guanajuato. Late Hemphillian.

Diagnosis—M^1 has subequally bilobed anterocone with a moderately deep anteromedian groove; M_1 bilobed only in the earliest stages of wear. Tendency to retain short, narrow mesoloph in M^1; no auxiliary lophs or lophids in other teeth. M^3s large. Size intermediate between that of *Calomys baskini* and *Calomys elachys/Baiomys kolbi.*

Etymology—*winklerorum* for doctors Dale and Alisa Winkler.

Description—M^1: The occlusal outline is oval, longer than it is wide, and narrow anteriorly. The labial cusps are tall, narrow, and slightly posterior relative to the lingual cusps. The posterior sides of cusps are vertical, anterior sides gently sloping. Lingual cusps wear first on their near-vertical medial faces, buccal cusps on posteromedial faces. Valleys between the cusps are deep, rounded, and partially closed by low cingula, which can bear stylar cuspules. Lingual cusps have arms extending anteriorly, forming an incipient mure. The anterocone is broad and bilobed. The anteromedian groove of the anterocone is short, but deep. The paracone has a small arm extending posteriorly to meet the anterior arm of the hypocone. A small mesostyle is present on one out of three specimens (Plate 1, J), the other two showing only a small swelling on the anterior arm of the hypocone (Plate 1, K, L). Arms off the hypocone and metacone join to form a tall posterior tooth margin. There is no posterior cingulum. One prominent root extends anteriorly of the anterocone; another extends downward on the lingual side from between the protocone and hypocone; a third root was presumably present but is not preserved.

M^2: The occlusal outline is a rounded trapezoid, distorted from rectangular by the prominent anterior slope of the protocone. The cusps and lophs are similar to those of M^1 but without an anterocone. A long, prominent anterior cingulum with a straight anterior margin is connected to the anterior arm of the protocone at an angle of about 120°, then extends transversely to the buccal margin, forming a basin between it and the paracone. A short posterior cingulum extends from the posterior arm of the hypocone, forming a basin between it and the medial arm of the metacone. No roots are preserved.

M^3: The occlusal outline is rounded, triangular to trapezoidal. The three main cusps—paracone, protocone, and hypocone, confluent with a reduced metacone—are joined to form a deep central valley. This main valley is restricted on its labial margin but open until advanced wear. A long anterior cingulum extends from the protocone to the labial edge, forming a basin, of variable length and depth, with the paracone. A small lingual valley between the protocone and hypocone is also of variable length and depth. No roots are preserved.

M_1: The occlusal outline is elongate, triangular to ovate with a relatively narrow, pointed anteroconid and broad, flat posterior margin. The cusps are robust, valleys between them are wide and rounded. Lingual cusps are placed anteriorly relative to labial cusps. The lingual cusps wear on their anterior faces to subvertical facets, whereas the labial cusps develop anteriorly-directed subhorizontal medial facets. The anteroconid wears first on its posterior face. The anteroconid is narrow, a single cusp, though possibly bilobed when unworn. An anterior cingulum is present as a narrow, posterolabially-directed arm off the anteroconid, forming an angled valley between it and the protoconid. This cingular valley becomes more pronounced with wear. A short, shallow anterolingual valley develops between the anteroconid and metaconid, which can form, in unworn specimens, a single arcuate structure by connecting with the longer, wider, cingular valley. The lingual valley between the metaconid and entoconid is deep and open. The protoconid and hypoconid have anterior and posterior medial arms, connecting at the midline with shorter medial arms from the metaconid and entoconid to form a mure. All three specimens lack a mesolophid or ectolophid. The posterior arm of the hypoconid extends transversely to form a tall posterior cingulum, with a valley between it and the entoconid. The posterolabial valley is wide and deep, partially closed by a low cingular shelf which can have cingular stylids. One specimen preserves a robust transverse posterior root.

MEASUREMENTS (in mm)

		N	X	Range
M^1	length	3	1.56	1.52–1.60
	posterior width	2	0.96	0.88–1.04
M^2	length	1	1.18	
	anterior width	1	1.06	
M^3	length	1	0.86	
	anterior width	1	0.98	
M_1	length	3	1.36	1.34–1.38
	posterior width	3	0.75	0.74–0.76

Remarks—The M^1 from GTO 2b is slightly wider than the two from GTO 2a, but was chosen as the type because of its good preservation.

Calomys winklerorum falls into an isolated size class (Figure 5), so it is relatively easy to distinguish from the other El Ocote rodents. A distinctive M_3 from the Concha fauna described by Lindsay and Jacobs (1985; IGCU 1192) and ascribed by them to *Calomys* sp. indet. falls into this same intermediate size category, but is slightly too large to assign to *Calomys winklerorum* without query. Unfortunately, no M_2s or M_3s of *Calomys winklerorum* have yet been recovered. An unpublished mandible fragment (IGCU 5823) with M_{1-3} from the Blancan of Guanajuato locality number GTO 5, bears an M_1 slightly narrower than those of *Calomys winklerorum* but within an allowable range of variation.

Calomys yahzi and *C. gidleyi*, described by Baskin (1979) from the older White Cone fauna of Arizona, are close to *Calomys winklerorum* in size, but differ from it in possessing a short, round, conspicuous anterocone on M^1 (a primitive feature) and a bilobed anteroconid on m_1. *Calomys winklerorum* is more derived in having longer teeth, and the anterocone is sufficiently wide that the lingual margin tapers smoothly.

Calomys arizonae (Gidley, 1922; Czaplewski, 1987), from the early Blancan Verde Formation of Arizona, strongly resembles *C. winklerorum* in size and essential features. *C. arizonae*, however, is higher-crowned, to the extent that the M_1 anteroconid remains bilobed with moderate wear, and has no accessory lophs or lophids. *C. winklerorum* shows no sign of a shortened posterior cingulum in M_1, characteristic of *C. arizonae*.

The material assigned to *Calomys winklerorum*, in the absence of jaw material, M_3s, and a larger sample size, may be a composite sample. It is unusual for *Calomys* to combine an M^1 with a bilobed anterocone and a mesoloph, with an M_1 possessing a single-cusped anteroconid and no auxilliary cuspids or lophids. The recovery of a larger sample of teeth, especially from GTO 2b, and further skull and jaw material would be helpful in clarifying the Hemphillian radiation of this abundant genus.

Calomys (Bensonomys) elachys Lindsay and Jacobs, 1985
(Plate 2, A, B)

Type specimen—IGCU 1174, right M^1 from the Concha fauna, UALP locality Y35 (CH-13), Chihuahua.

Referred material—Two isolated upper first molars. From GTO 2a: IGCU 7276. From GTO 2b: IGCU 7272.

Range—UALP localities Y3 (CH-11), Y39 (CH-15), and Y35 (CH-13), Yepómera and Concha faunas, Chihuahua. IGCU localities GTO 2a and 2b, El Ocote fauna, Guanajuato. Late Hemphillian, early Blancan.

Diagnosis—As in Lindsay and Jacobs, 1985.

MEASUREMENTS (in mm)

		N	X	Range
M^1	length	2	1.41	1.40–1.42
	posterior width	2	0.87	0.86–0.88

Remarks—13 isolated teeth from El Ocote fall into the same size class (Figure 5) and closely resemble those described by Lindsay and Jacobs (1985) from the Yepómera fauna as *Calomys elachys* and *Baiomys kolbi*. Lindsay and Jacobs observed that the two species are distinguished from each other "with great difficulty". From the set of 13 molars, only two M^1s have been distinguished as *C. elachys*, based on the distinctive offset cusps of the strongly bilobed anterocone. The cusps incline posteriorly and the buccal cusp is more posterior than the lingual cusp, to the extent that a shelf is formed at the base of the anterocone which can bear small stylar cuspules. The two lobes of the anterocone remain separated and offset through moderate wear. In addition, the two molars assigned to *C. elachys* have more pronounced mesolophs than *B. kolbi*.

The features of the anterocone described here are more extreme than in the type of *C. elachys* from Yepómera, and suggest a possible relationship with the unusual small rodent from GTO 2a (IGCU 7275, discussed below).

Baiomys kolbi Hibbard, 1952
(Figure 6; Plate 2, C, D)

Type specimen—UMMP 24846, right dentary with incisor and M_{1-3} from the Fox Canyon fauna, locality UM-K1-47, Meade County, Kansas (Hibbard, 1952, p. 201).

Referred material—Two isolated upper first molars. From GTO 2a: IGCU 7274. From GTO 2b: IGCU 7271.

Range—Fox Canyon fauna, Kansas; IGCU localities CH-11, CH-15, and CH-13 (UALP Y3, Y39, Y35), Yepómera and Concha faunas, Chihuahua; IGCU localities GTO 2a and GTO 2b, El Ocote fauna, Guanajuato. Late Hemphillian and early Blancan.

Diagnosis—As in Hibbard (1952), amended with the addition of upper dentition by Lindsay and Jacobs (1985)

MEASUREMENTS (in mm)

		N	X	Range
M^1	length	2	1.36	1.34–1.38
	posterior width	2	0.84	0.82–0.86

Remarks—These two M^1s were assigned to *B. kolbi* rather than to *C. elachys* based on the following criteria: the bilobed anterocone is oriented transversely, and the lobes are confluent with little wear; there is no anterior shelf nor styler cuspules on the anterocone. *B. kolbi* is not readily distinguishable from *Calomys elachys*, and there may be other small cricetids within this size class and with similar teeth which complicate sorting and identification. Until these problems are resolved by further comparisons and a better sample, identifications of rodents of this size class should be considered tentative.

Calomys elachys and/or *Baiomys kolbi* undifferentiated

Type specimens, range, diagnosis—As above.

Referred material—nine isolated molars. From GTO 2a: broken M^1 (IGCU 7273), M^2 (7310), four M_1s (7262, 7267, 7268, 7025), M_2 (7153). From GTO 2b: M^2 (7311), M_2 (7380).

MEASUREMENTS (in mm)

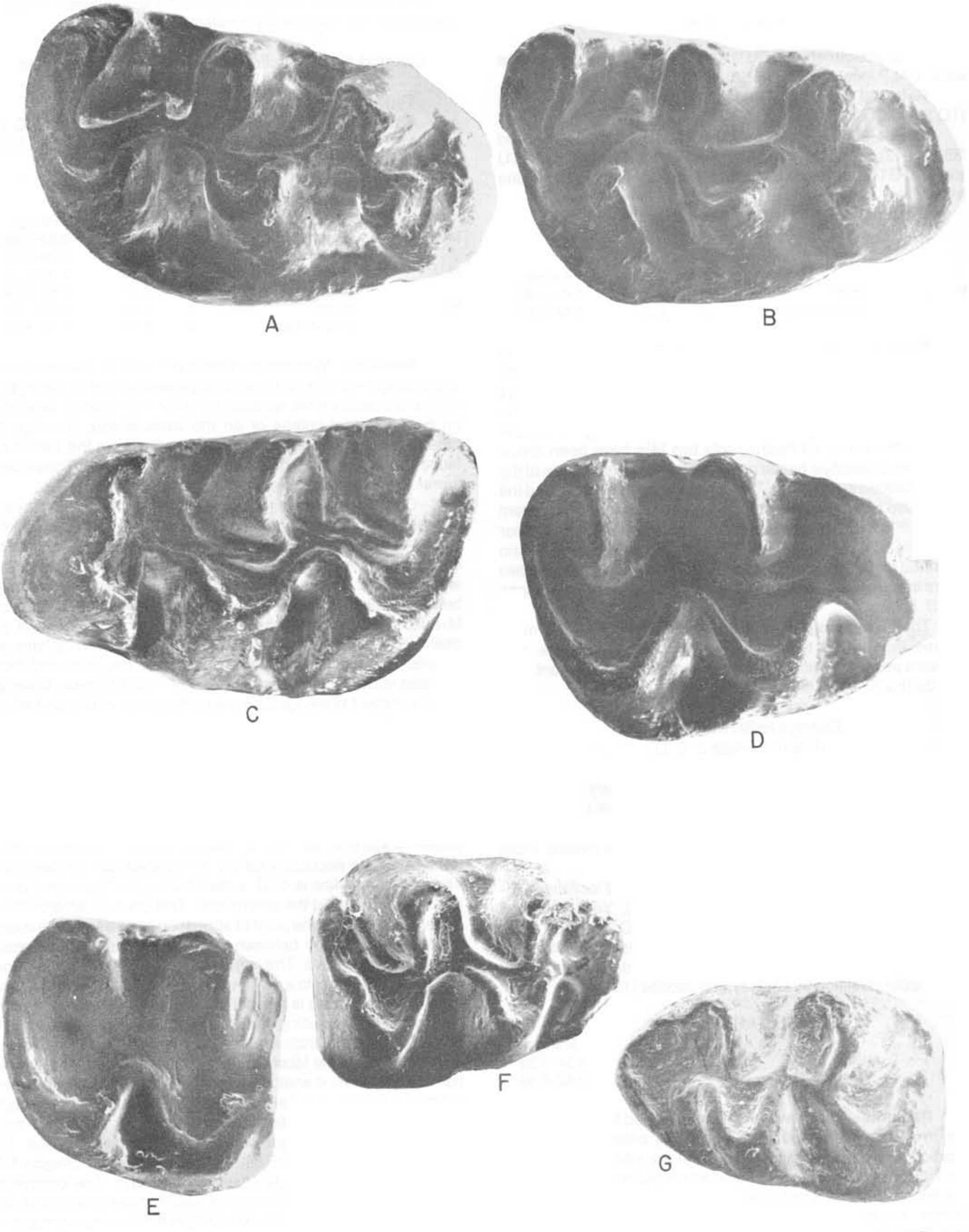
		N	X	Range
M^2	length	2	0.86	0.84–0.88
	anterior width	2	0.79	0.76–0.82
M_1	length	4	1.14	1.02–1.24
	posterior width	3	0.67	0.62–0.74
M_2	length	2	0.93	0.86–1.00
	anterior width	2	0.77	0.72–0.82

Remarks—With the exception of the M^1s, the small teeth of this size class (Figure 5), including specimens of *C. elachys, B. kolbi* and possibly more species, were not satisfactorily separable on morphological criteria or on the basis of size (average M_1 measurements for samples of both species from the Yepómera fauna are represented by squares on Figure 5, D). These teeth therefore remain undifferentiated.

One simple discriminating feature described by Lindsay and Jacobs (1985) is that the anteroconid on the M_1 of *C. elachys* is large and broadly separated from the metaconid; whereas the M_1 of *B. kolbi* is more anteroposteriorly compressed, so that the anteroconid is slightly smaller than the metaconid and the valley between them is narrow. This would indicate that both little-worn M_1s from El Ocote are ascribable to *B. kolbi*. In general appearance the higher-crowned *B. kolbi* should remain lophate and angular with wear, while the cusps should be wider and more rounded in *C. elachys*. The sample size from El Ocote, however, is not sufficient to recognize subtle differences in M^2s and M^3s.

Cricetid, gen. et sp. indet.
(Figure 6; Plate 2, J, K)

One isolated, slightly worn left M^1 from GTO 2a (IGCU 7275) falls in the lower range of the *Calomys elachys/Baiomys kolbi* size cluster (Figure 5, A), but is morphologically distinctive. More material will be necessary before the species can be described. The occlusal outline is oval, widest across the hypocone, ovate and asymmetrical at the anterocone. This unusual anterocone is large and bilobed to the point of appearing as two separate cusps. There is a flat valley between them rather than the customary anteromedian groove. The lingual cusp of the anterocone is low, elongate, and wears to a crest, with a shallow groove on its lingual side. The labial cusp is tall, narrow, and relatively free-standing. Lingual cusps (including that of the anterocone) wear to sub-horizontal facets, inclined toward the midline. Labial cusps develop sub-vertical facets on their posterior faces. The orientation of wear facets is analogous to that of other cricetids, but more extreme in this strongly terraced tooth. Labial cusps are dominant. The tallest cusps, in order, are: the metacone, paracone, labial anterocone, hypocone, protocone, and lingual anterocone. The valleys appear wider and shallower than in other cricetid M^1s because they are strongly offset longitudinally. The protocone-anterocone valley, and the central valley of the anterocone, are not well defined because the terracing obscures enamel margins. All cusps slope anteriorly. The small cingular shelves on the valley margins bear stylar cusps, and there is a nub of a mesoloph. A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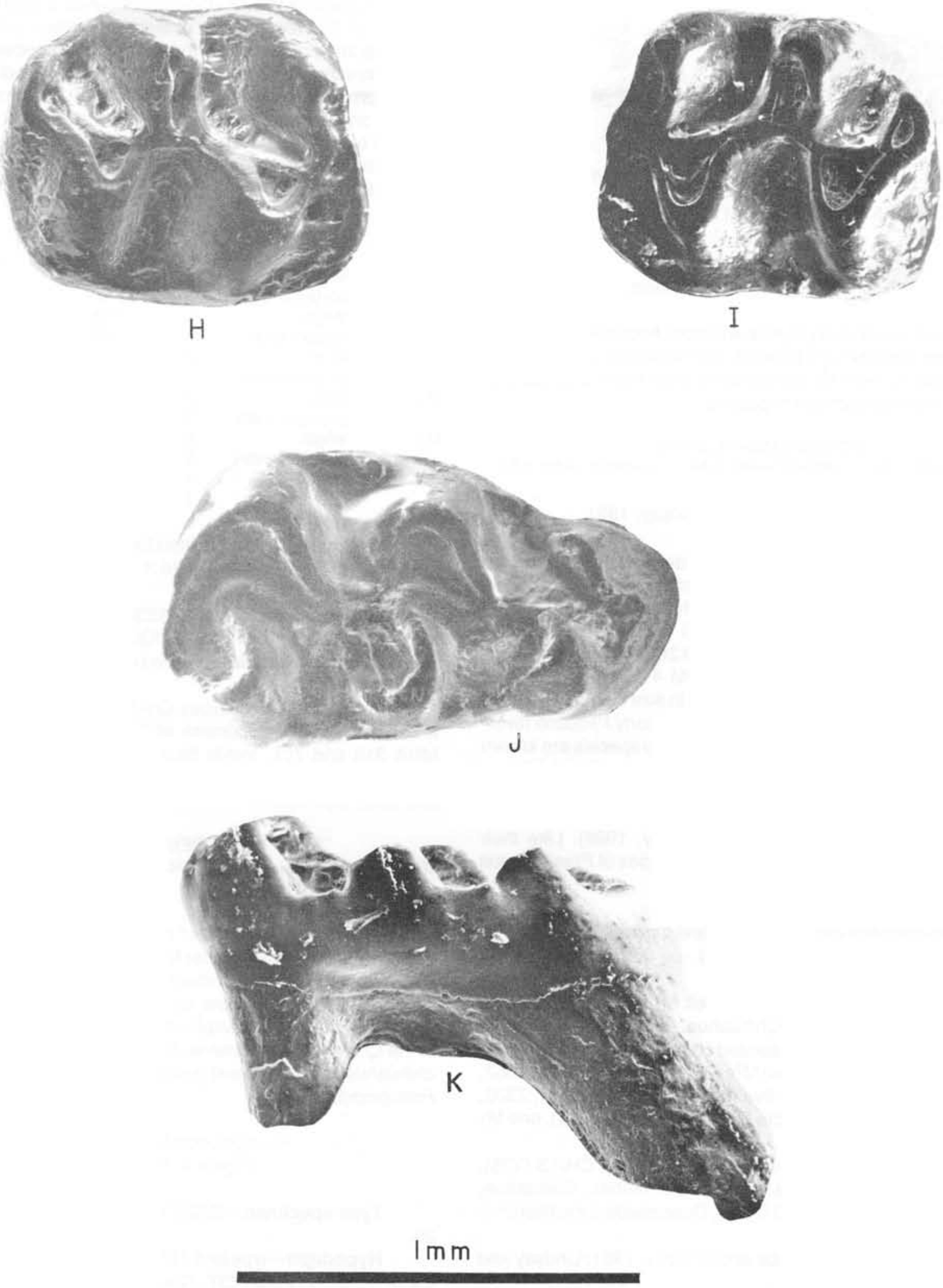


Plate 2.- Orientation as in Figure 4. All to same scale. A—*Calomys elachys*, IGCU 7272, right M^1; B—*Calomys elachys*, IGCU 7276, right M^1; C—*Baiomys kolbi*, IGCU 7271, left M^1; D—*Baiomys kolbi*, IGCU 7274, right M^1; E—*C. elachys* or *B. kolbi*, IGCU 7311, right M^2; F—*C. elachys* or *B. kolbi*, IGCU 7262, right M_1; G—*C. elachys* or *B. kolbi*, IGCU 7267, left M_1; H—*C. elachys* or *B. kolbi*, IGCU 7153, right M_2; I—*C. elachys* or *B. kolbi*, IGCU 7380, left M_2 J—Cricetid, gen. et sp. indet., IGCU 7275, left M^1, occlusal view; K—Cricetid, gen. et sp. indet., IGCU 7275, left M^1, buccal view.

cricetids

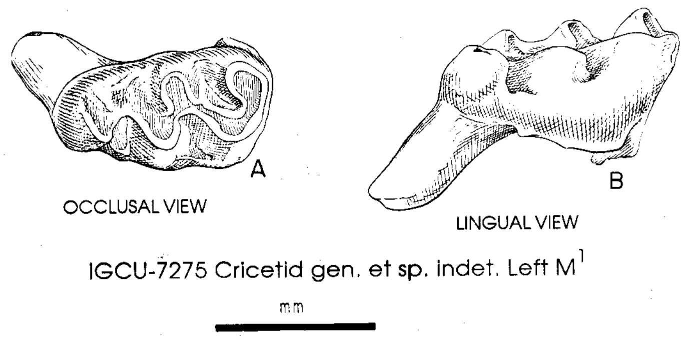


Figure 6. Cricetid, gen. et sp. indet.

long, wide, cylindrical root projects anteriorly from the anterocone; a thinner root departs from beneath the metacone; a third root is not preserved, but can be presumed to have been wide but flat, originating from beneath the hypocone.

MEASUREMENTS (in mm)

M^1 length: 1.34 anterior width: 0.52 posterior width: 0.84

Prosigmodon Jacobs and Lindsay, 1981

Prosigmodon is believed to be derived from *Calomys* (Lindsay and Jacobs, 1985). The oldest known record of this genus is probably from the Coffee Ranch fauna of Texas, which is slightly older than Yepómera and El Ocote, and produces *Prosigmodon chihuahuensis* (TMM 41261-40) and an undescribed species of *Prosigmodon* (TMM 41261-44, -45; initial identification by E. Lindsay) intermediate in size between the new species described here and *P. oroscoi.* The early Pliocene diversification of *Prosigmodon* is conspicuous. Two species are known from the Yepómera fauna; the genus occurs in the Concha fauna (Lindsay and Jacobs, 1985), in the Verde fauna of Arizona (Czaplewski, 1987) and in the Blancan Truth or Consequences fauna of New Mexico (Repenning and May, 1986). Like their modern relative, the cotton rat *Sigmodon*, species of *Prosigmodon* tend to be abundant wherever they occur.

Prosigmodon oroscoi Jacobs and Lindsay, 1981
(Plate 3, A-E)

Type specimen—IGCU 1217, left M^1 from the Yepómera fauna (IGCU locality CH-15), Chihuahua.

Referred material- 17 isolated cheek teeth. From GTO 2a: two M^{1}s (IGCU 7244, 7247); two M^{2}s (7288, 7282); two M^{3}s (7352, 7355); two M$_1$s (7023, 7210); five M$_2$s (7319, 7329, 7331, 7332, 7338); and one M$_3$ (7374). From GTO 2b: one M^1 (7241), one M$_1$ (7214), and one M$_2$ (7346).

Range—IGCU localities CH-11 (UALP Y3), CH-13 (Y35), and CH-15 (Y39), Yepómera and Concha faunas, Chihuahua; IGCU GTO 2a and GTO 2b, El Ocote, Guanajuato. Late Hemphillian and early Blancan.

Diagnosis—As in Jacobs and Lindsay, 1981; Lindsay and Jacobs, 1985.

Description—As in Jacobs and Lindsay, 1981; Lindsay and Jacobs, 1985. Both the Yepómera-Concha and El Ocote samples show the frequent development of a posteriorly-directed spur or lophule off the posterior face of the paracone (paralophule, in the terminology of Hershkovitz, 1962) on M^1 and M^2. This feature becomes obscured with wear.

Remarks—*Prosigmodon oroscoi* overlaps with the lower size range of the new species described below (Figure 5, A-F), but its proportions differ sufficiently to define a distinct field (*e.g.*, the M^{2}s of *P. oroscoi* have a slightly narrower posterior width relative to anterior width than those of the new species). *P. oroscoi* falls in the same size class as *Calomys baskini*, but differs in some proportions and numerous morphological features. M^{2}s of *P. oroscoi* and *C. baskini* were separated easily on the basis of occlusal outline, as noted above. The M$_2$s were separated mainly on the basis of crown height, which is greater in *P. oroscoi* than in *C. baskini*.

MEASUREMENTS (in mm)

		N	X	S	Range
M^1	length	3	1.87		1.84–1.92
	posterior width	3	1.29		1.24–1.36
M^2	length	2	1.42		1.38–1.46
	anterior width	2	1.25		1.24–1.26
M^3	length	2	1.16		1.14–1.18
	anterior width	2	1.14		1.10–1.18
M$_1$	length	3	1.81		1.76–1.84
	posterior width	2	0.98		0.96–1.00
M$_2$	length	5	1.41	0.02	1.38–1.44
	posterior width	5	1.24	0.04	1.20–1.28
M$_3$	length	1	1.38		
	anterior width	1	1.26		

Prosigmodon chihuahuensis Lindsay and Jacobs, 1985
(Plate 3, R)

Type specimen—IGCU 1238, left dentary fragment with M$_{1-2}$, from the Yepómera fauna (IGCU CH-15).

Referred material—Isolated left M^2 (IGCU 7290) from GTO 2b.

Range—IGCU localities CH-14 (UALP Y37), CH-15 (Y39), and CH-17 (Y40), Yepómera and Concha faunas, Chihuahua; MNA 318 and 701, Verde fauna, Arizona (Czaplewski, 1987); possibly TMM 41261, Coffee Ranch fauna, Texas; IGCU GTO 2b, El Ocote, Guanajuato. Late Hemphillian and early Blancan.

MEASUREMENTS (in mm)

M^2 length: 1.60 anterior width: 1.84 posterior width: 1.58

Remarks—The single, moderately well-worn specimen from El Ocote is the largest of many *Prosigmodon* teeth, plotting well outside the range of other M^{2}s (Figure 5, B). It is indistinguishable from *Prosigmodon chihuahuensis* described by Lindsay and Jacobs (1985). The roots of this specimen are incompletely preserved, but there is evidence of a central, accessory rootlet, as in the Chihuahua specimens. If this tooth is correctly defined, *P. chihuahuensis* is the most widespread and long-lived species of *Prosigmodon.*

Prosigmodon ferrusquiai n. sp.
(Figure 4; Plate 3, F-Q)

Type specimen—IGCU 7254, isolated right M^1, from GTO 2a.

Hypodigm—type and 125 isolated cheek teeth. From GTO 2a: M^{1}s: IGCU 7236, 7237, 7243, 7245, 7248, 7249, 7250, 7251, 7253, 7255, 7257, 7258, 7259, 7260, 7261, and SMU 14-71238, -71239, -71240, -71252, -71256; M^{2}s: IGCU 7022, 7280, 7281, 7283, 7284, 7285, 7286, 7287, 7297, 7298, 7299, 7302, 7303, 7304, 7305, 7306, and SMU 14-71291, -71292, -71293, -71294, -71295; M^{3}s: IGCU 7168, 7353, 7354, 7356, 7357, 7358, 7359, 7360, 7361, 7362, and SMU 14-71347, -71348, -71349, -71350; M$_1$s: IGCU 7001, 7002, 7203, 7204, 7205, 7206, 7207, 7208, 7211, 7213, 7216, 7217, 7218, 7219, 7220, 7221, 7222, 7223, 7224, 7225, 7264, and SMU 14-71226, -71228, -71229, -71230; M_2s: IGCU 7301, 7317, 7318, 7321, 7322, 7324, 7325, 7326, 7328, 7333, 7334, 7335, 7336, 7337, 7339, 7340, and SMU 14-71341, -71342, -71343, -71344, -71345; M_3s: IGCU 7026, 7370, 7371, 7372, 7373, 7374, 7375, and SMU 14-71364, -71367, -71368. From GTO 2b: M^1: IGCU 7242; M^2s: IGCU 7289, 7300; M^3s: IGCU 7363, and SMU 158-71351; M_1s IGCU 7204, 7215, 7227; M_2s: IGCU 7316, 7320, 7327; M_3s: IGCU 7366, and SMU 158-71365.

Range—IGCU sections GTO 2a and GTO 2b, El Ocote, Guanajuato; late Hemphillian.

Diagnosis—Anteroconid on M_1 weakly bilobed when unworn. Little development of posterior lophules. Accessory rootlets rare. Size intermediate between that of *Prosigmodon oroscoi* and *Prosigmodon chihuahuensis* (Figure 5, A-F).

Etymology—*ferrusquiai* for doctor Ismael Ferrusquía-Villafranca, vertebrate paleontologist and professor of the Universidad Nacional Autónoma de México.

Description—In upper molars, unworn cusps are rounded, and lingual cusps are set anterior to corresponding labial cusps. Posterior cusp faces are nearly vertical, while anterior faces are sloping. Wear facets develop on the posterior faces of the labial cusps (metacone, paracone, anterocone if present), and on the medial faces of the lingual cusps (protocone and hypocone). In unworn lower molars, the anterior sides of the cusps are subvertical, and the posterior sides sloping. Wear facets are initiated on the anterior faces of the lingual cusps, and on the medial faces of the labial cusps. The anteroconid of M_1 develops a wear facet on its posteromedial side. Lingual cusps on the uppers are especially high-crowned. Lingual valleys are consequently deeper and narrower than labial valleys.

M^1: The occlusal outline is oval, with flattened posterior margin, tapering anteriorly to a rounded anterior margin. The tooth is relatively broad with a wide, round anterocone. The anterocone slopes gently both posteriorly and anteriorly, and is subequally bilobed, with the labial lobe slightly taller; a short anteromedian groove is obscured by advanced wear. The lingual valleys are deep and narrow; the labial valleys are less deep, more open, and rounded. Labial valleys are partially enclosed by a low cingular shelf, which is less developed on the lingual side. The protocone and hypocone have long, anteromedial arms, oriented along the midline, connecting the cusps in an incipient mure. A short posteromedial arm from the protocone links with the anterior arm of the hypocone and medial projections from the paracone. The short posteromedial arm of the hypocone connects with the metacone to form a tall posterior margin. Eight out of 20 M^1s have some form of protuberance entering the posterolabial valley, either off the posterior mure (mesoloph), or off the posterior face of the paracone (paralophule). This feature is never strongly developed and is obscured with wear. There are three robust roots; one specimen (IGCU 7258) preserves in addition a small accessory rootlet beneath the paracone.

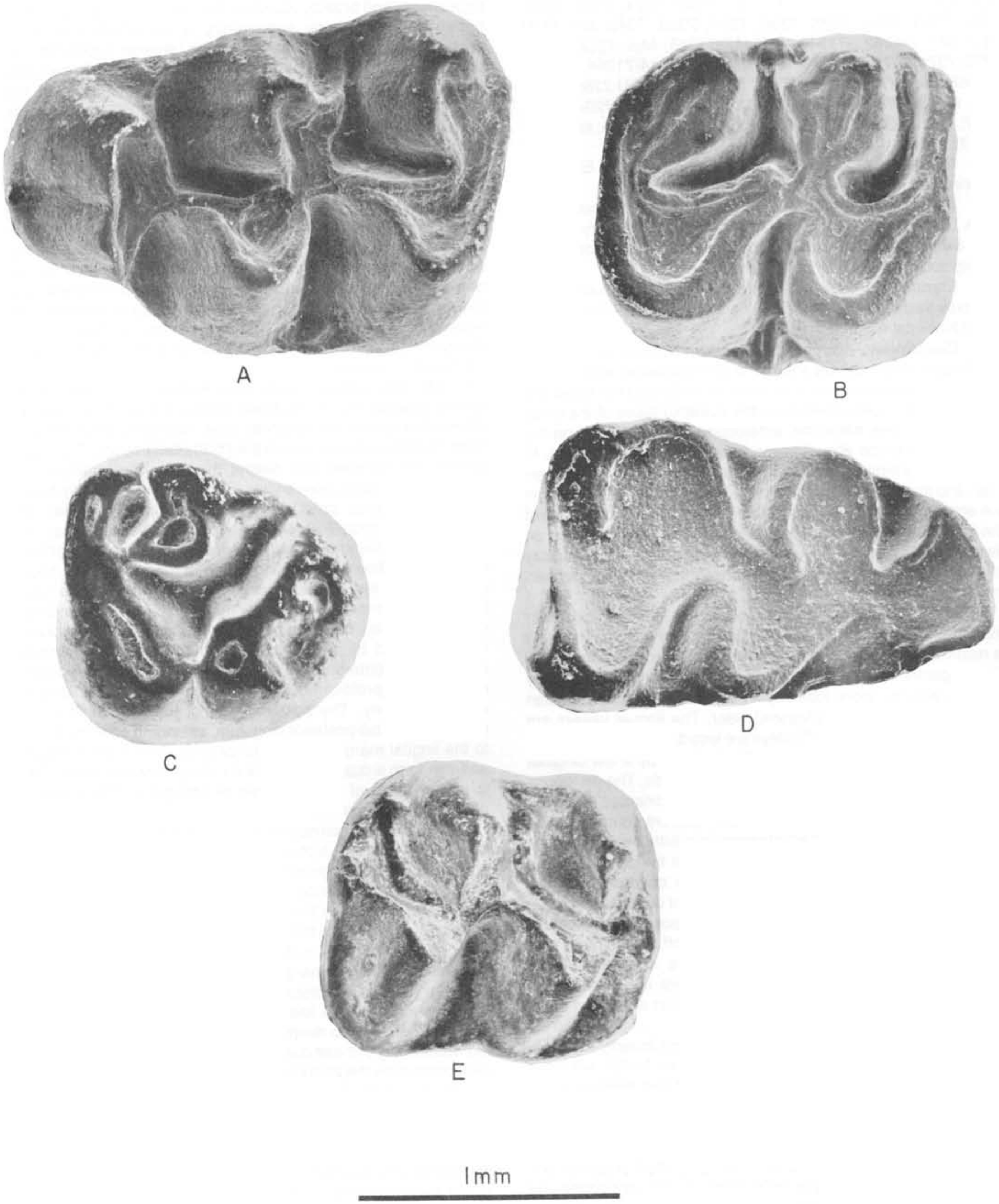
M^2: The occlusal outline is quadrate and broadly rounded. Cusps and lophs are similar to those described for M^1, but there is no anterocone. The anteromedial arm of the protocone terminates in an anterior cingulum, which forms an anterior wall from the midline to the labial margin. Wear facets tend to be more horizontal than in M^1 and there is less of a tendency to develop protuberances in the posterolabial valley. A short posterior cingulum originates from the posteromedial arm of the hypocone and runs from the midline halfway to the labial margin; this remains conspicuous through the early stages of wear. There are three robust roots, with no indication of rootlets.

M^3: The occlusal outline is variable, from triangular to trapezoidal, and broadly rounded. The anterior margin is slightly flattened. The general appearance is asymmetrically heart-shaped, defined by a large protocone, smaller hypocone and paracone, and a low metacone. A deep central basin is enclosed lingually by a posterior arm of the protocone meeting the hypocone, and partially enclosed labially by a confluence of spurs from the paracone and metacone, sometimes with a low labial cingulum. A labially-directed spur off the medial arm of the hypocone forms a short loph in the central basin, obscured with advanced wear. The anterior cingulum extends labially from the protocone to the margin, forming a shallow anterior basin between it and the short transverse arm of the paracone. The anterior basin reduces with moderate wear to an eyelet in the anterolabial corner, and disappears with advanced wear. A posterior basin is formed between the transverse loph of the hypocone and metacone, and the short, arcuate posterior cingulum. This basin reduces with wear to an eyelet at the midline of the posterior platform, then disappears with advanced wear. There are three robust roots, no indication of rootlets.

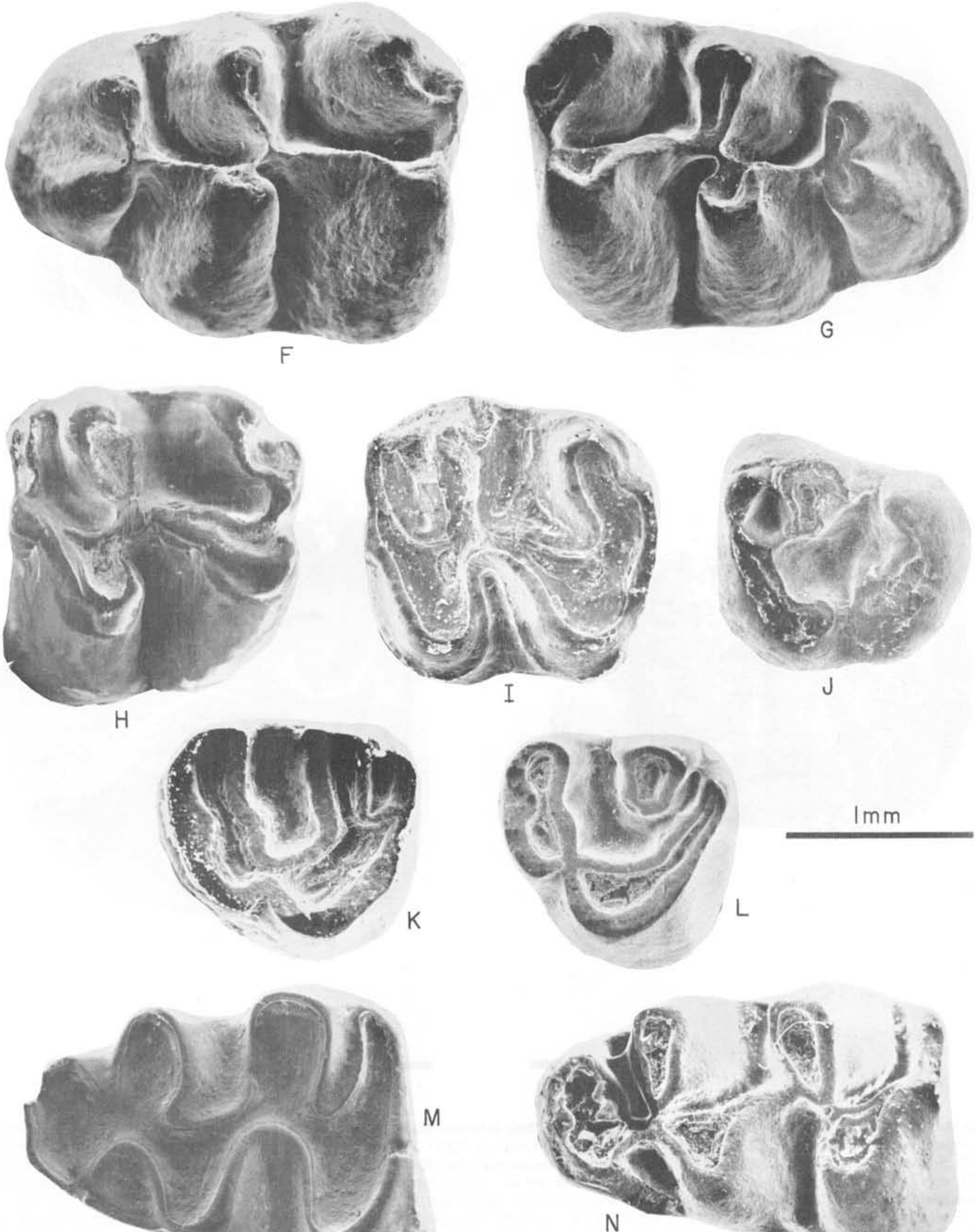
M_1: The occlusal outline is an elongate, rounded triangle, narrowing anteriorly to a rounded anterior margin. The cusps are moderately robust with relatively wide, rounded valleys between them. The lingual cusps are anterior of the labial cusps. The lingual valleys are narrower and deeper than the labial valleys. The anteroconid is wide, frequently subequally bilobed, rarely single-lobed; the bilobed state is most evident with slight wear. The anteromedian groove rarely persists with advanced wear. The unworn tip of the anteroconid is frequently rugose. The anterior cingulum, confluent with the labial side of the anteroconid, tapers posteriorly to the anterior base of the protoconid. The valley between the anteroconid and the metaconid is narrow and shallow, but persists into advanced wear. The anteroconid is linked to the metaconid by a short, relatively robust, antero-posterior anterolophid (anteromedial arm of the metaconid). The anterior arms of the protoconid and hypoconid are short, directed anteroposteriorly. The posterior arm of the hypoconid is continuous with a tall posterior cingulum, extending from the midline to the lingual margin. The posterior cingulum thickens medially and can form a cuspule which does not persist with wear. There is no indication of a mesolophid or ectolophid. There are two robust roots, no rootlets.

M_2: The occlusal outline is a rounded rectangle, longer than it is wide. The cusps, lophs, and roots are similar to those in M_1, but without the anteroconid and associated structures. The anterior cingulum is short and narrow, forming an anterior wall from the metaconid to the labial margin, as a thin ridge directly anterior of and close to the protoconid.

M_3: The occlusal outline is a rounded triangle to trapezoid with a straight anterior margin, narrowing posteriorly to an arcuate posterior margin. The protoconid, metaconid, and hypoconid are large, the entoconid is low, and there is a robust posterior cingulum. (There are no deeply worn specimens in this sample, so the wear history of these cusps remains unknown). The transverse metaconid joins the protoconid, forming an anterior wall. There is a minute anterior cingulum near the midline, anterior of the metaconid; its development is variable and it is quickly lost with wear. A deep, narrow, posterolabial valley is formed between the protoconid and its posterior arm, and the transversely-oriented hypoconid, whose anterior arm unites with the entoconid. A slightly less deep valley is formed on the anterolingual side, between the entoconid, the protoconid and its arm, and the metaconid. A straight posterior wall, directed slightly posterolingually-anterolabially, is formed by the transverse hypoconid giving rise



Prosigmodon



spp.

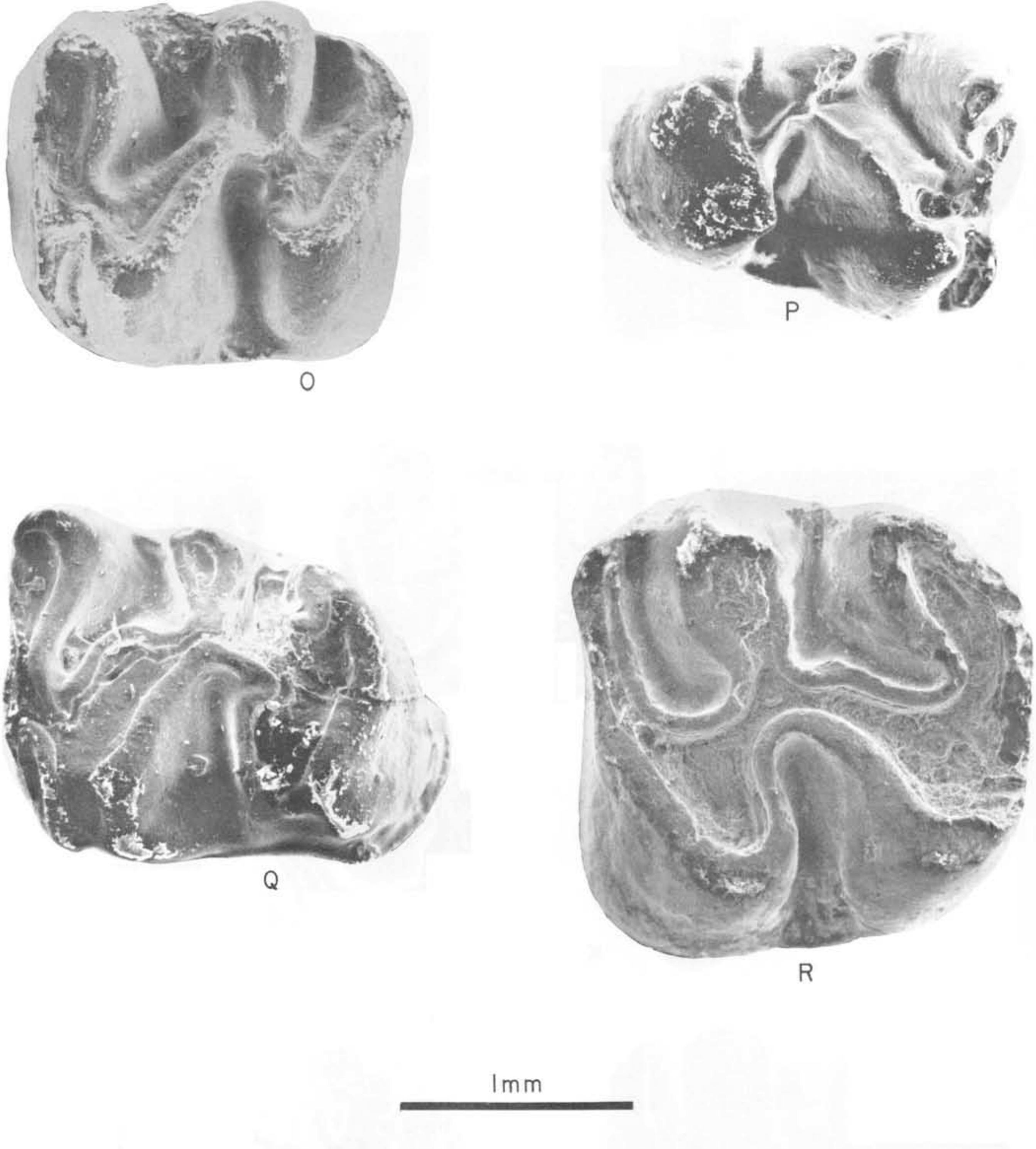


Plate 3.- Orientation as in Figure 4. A—E, F—N, and O—R are to their indicated scale, respectively. A—*Prosigmodon oroscoi*, IGCU 7244, left M^1; B—*Prosigmodon oroscoi*, IGCU 7288, right M^2; C—*Prosigmodon oroscoi*, IGCU 7355, left M^3; D—*Prosigmodon oroscoi*, IGCU 7210, right M$_1$; E—*Prosigmodon oroscoi*, IGCU 7329, right M$_2$; F—*Prosigmodon ferrusquiai* n. sp., IGCU 7237, left M^1; G—*Prosigmodon ferrusquiai* n. sp., type IGCU 7254, right M^1; H—*Prosigmodon ferrusquiai* n. sp., IGCU 7286, left M^2; I—*Prosigmodon ferrusquiai* n. sp., IGCU 7289, right M^2; J—*Prosigmodon ferrusquiai* n. sp., IGCU 7359, left M^3; K—*Prosigmodon ferrusquiai* n. sp., IGCU 7358, right M^3; L—*Prosigmodon ferrusquiai* n. sp., IGCU 7361, right M^3; M—*Prosigmodon ferrusquiai* n. sp., IGCU 7215, left M$_1$; N—*Prosigmodon ferrusquiai* n. sp., IGCU 7220, left M$_1$; O—*Prosigmodon ferrusquiai* n. sp., IGCU 7318, left M$_2$; P—*Prosigmodon ferrusquiai* n. sp., IGCU 7371 right M$_3$; Q—*Prosigmodon ferrusquiai* n. sp., IGCU 7370, left M$_3$; R—*Prosigmodon chihuahuensis*, IGCU 7290, left M^2.

Prosigmodon spp.

to the posterior cingulum. A shallow valley formed between the posterior cingulum and the entoconid is sealed off by the posterior arm of the entoconid; this feature persists through moderate wear. No roots are preserved.

MEASUREMENTS (in mm)

		N	X	S	Range
M^1	length	22	2.23	0.12	1.96–2.40
	posterior width	22	1.53	0.09	1.40–1.72
M^2	length	23	1.54	0.09	1.34–1.72
	anterior width	23	1.40	0.07	1.26–1.54
M^3	length	16	1.30	0.07	1.18–1.46
	anterior width	16	1.19	0.05	1.10–1.28
M_1	length	25	2.02	0.13	1.92–2.28
	posterior width	24	1.30	0.11	1.24–1.48
M_2	length	23	1.63	0.09	1.42–1.79
	anterior width	23	1.45	0.08	1.20–1.60
M_3	length	12	1.54	0.07	1.44–1.62
	anterior width	11	1.29	0.06	1.20–1.42

Remarks—*Prosigmodon ferrusquiai* has the simplest morphology of the three Mexican species of *Prosigmodon*. M_1s and M_2s show little tendency to develop mesolophules or paralophules, or accessory rootlets, compared to *P. oroscoi* or (the most extreme case) *P. chihuahuensis*. The M^3s of *P. oroscoi* and *P. chihuahuensis* tend to have transverse spurs or connections occupying the central basin, while the central basin in *P. ferrusquiai* is always open and rarely accomodates transverse spurs (contrast Plate 3, J with K, L). The late Hemphillian to early Blancan trend defined by *Prosigmodon* species from Coffee Ranch, El Ocote, Yepómera, Verde, and Truth or Consequences is towards increased crown height, with elevation of the cingulum; and towards increased simplicity by elimination of accessory lophules and merging of the bilobed anterocone to a single loph.

There is no discernible difference between samples from GTO 2a and GTO 2b.

Tribe Neotomini

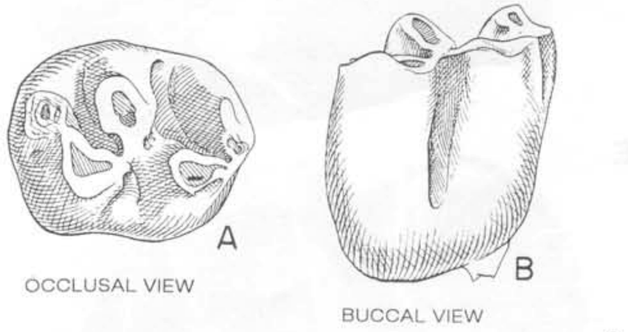
Neotoma (Paraneotoma)

Four subgenera of *Neotoma*, the woodrats, are usually recognized. In the fossil subgenus *Paraneotoma* there are currently four described species, all from the Pliocene of the central United States: *P. quadriplicatus* (Hibbard, 1941), *P. taylori* and *P. sawrockensis* (Hibbard, 1967), and *P. minutus* (Dalquest, 1983).

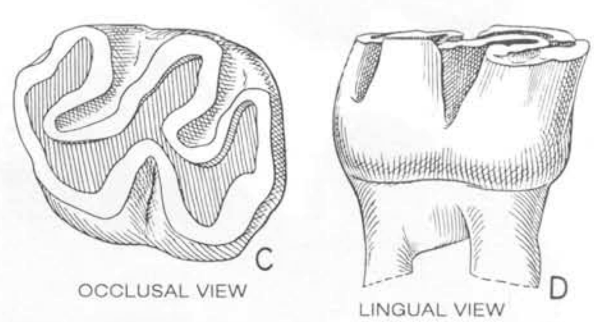
Neotoma (Paraneotoma) cf. *sawrockensis* Hibbard, 1967
(Figure 7; Plate 4, A-H)

Type specimen—UMMP 41396, a right M^1 from Saw Rock Canyon, Rexroad Formation, Seward County, Kansas. Paratype—UMMP 53782, a left M^2.

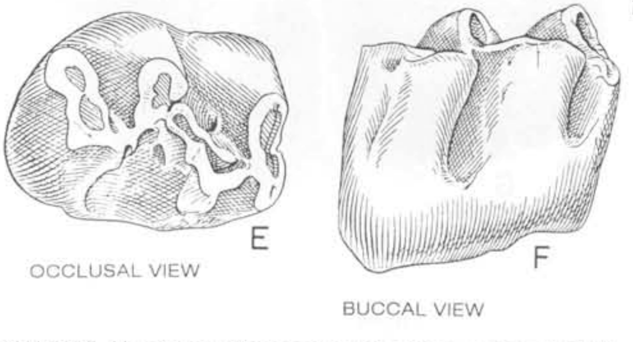
Referred material—Nine isolated molars. From GTO 2a: one M^2 (IGCU 7312); and two M_2s (7314, 7315). From GTO 2b: three M^3s (7170, 7171, 7172); and three M_1s (7231, 7232, 7233).



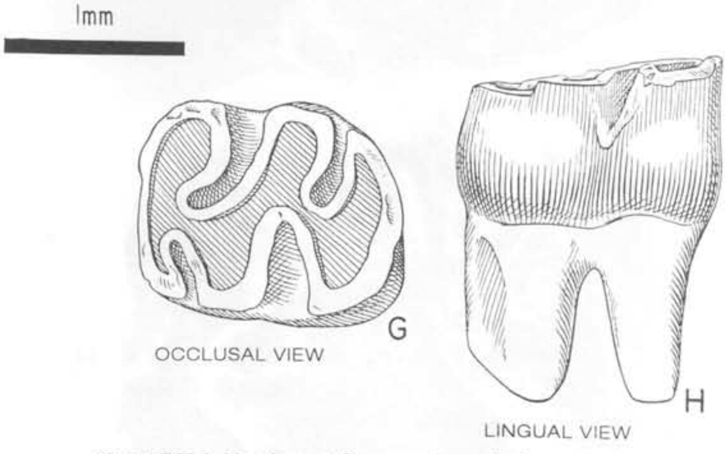
IGCU-7312, *Neotoma* (*Paraneotoma*) cf. sawrockensis LM^2



IGCU-7313, *Neotoma* (*Paraneotoma*) sp. indet. RM^2

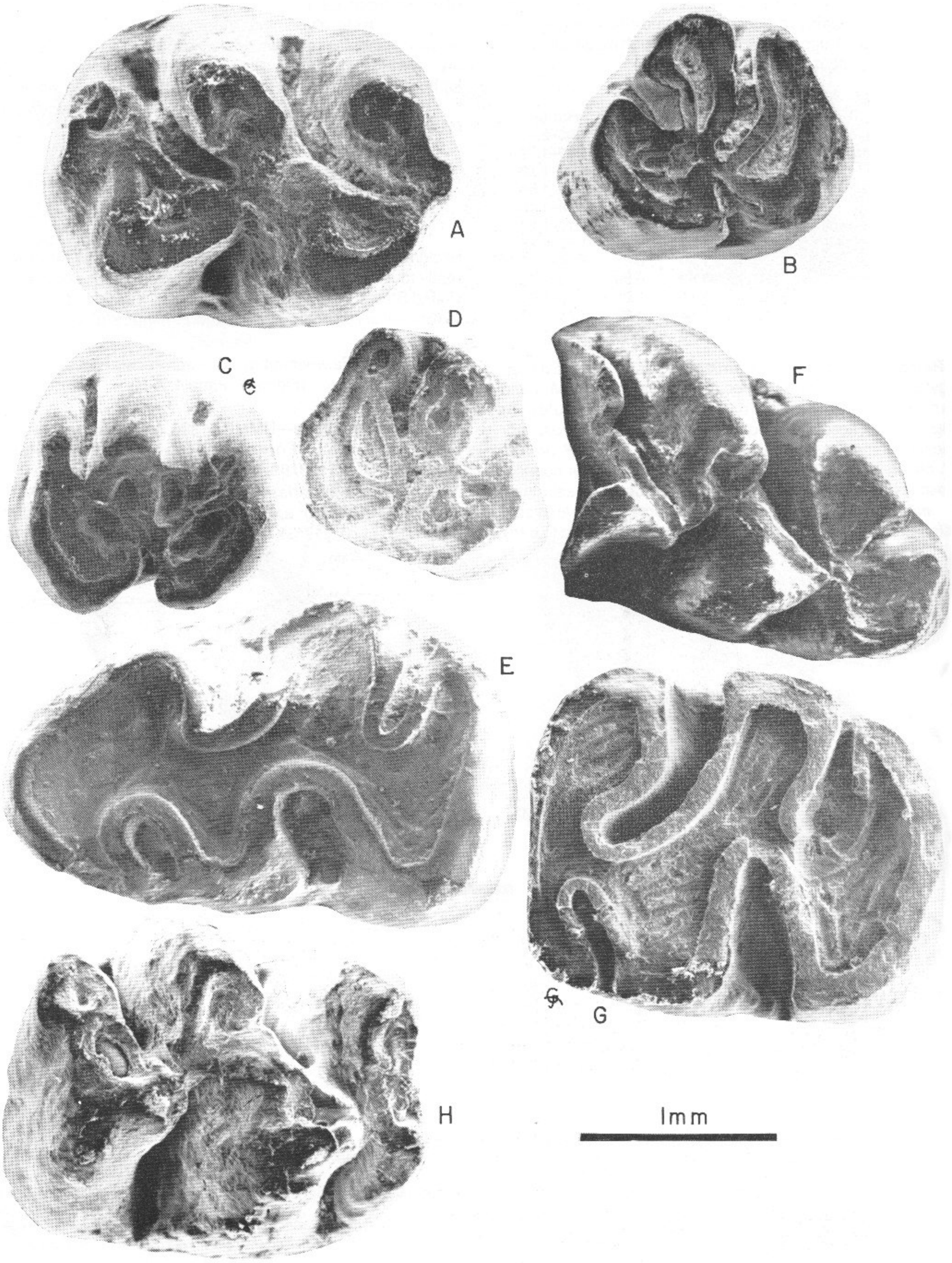


IGCU-7315, *Neotoma* (*Paraneotoma*) cf. sawrockensis RM_2



IGCU-7314, *Neotoma* (*Paraneotoma*) cf. sawrockensis LM_2

Figure 7.- *Neotoma (Paraneotoma)* spp., showing wear series and cusp heights. A—*Neotoma (Paraneotoma)* cf. *sawrockensis*, IGCU 7312, left M^2, occlusal view; B—*Neotoma (Paraneotoma)* cf. *sawrockensis*, IGCU 7312, left M^2, lingual view; C—*Neotoma (Paraneotoma)* sp. indet., IGCU 7313, right M^2, occlusal view; D—*Neotoma (Paraneotoma)* sp. indet., IGCU 7313, right M^2, buccal view; E—*Neotoma (Paraneotoma)* cf. *sawrockensis*, IGCU 7315, right M_2, occlusal view; F—*Neotoma (Paraneotoma)* cf. *sawrockensis*, IGCU 7315, right M_2, buccal view; G—*Neotoma (Paraneotoma)* cf. *sawrockensis*, IGCU 7314, left M_2, occlusal view; H—*Neotoma (Paraneotoma)* cf. *sawrockensis*, IGCU 7314, left M_2, lingual view.



Neotoma

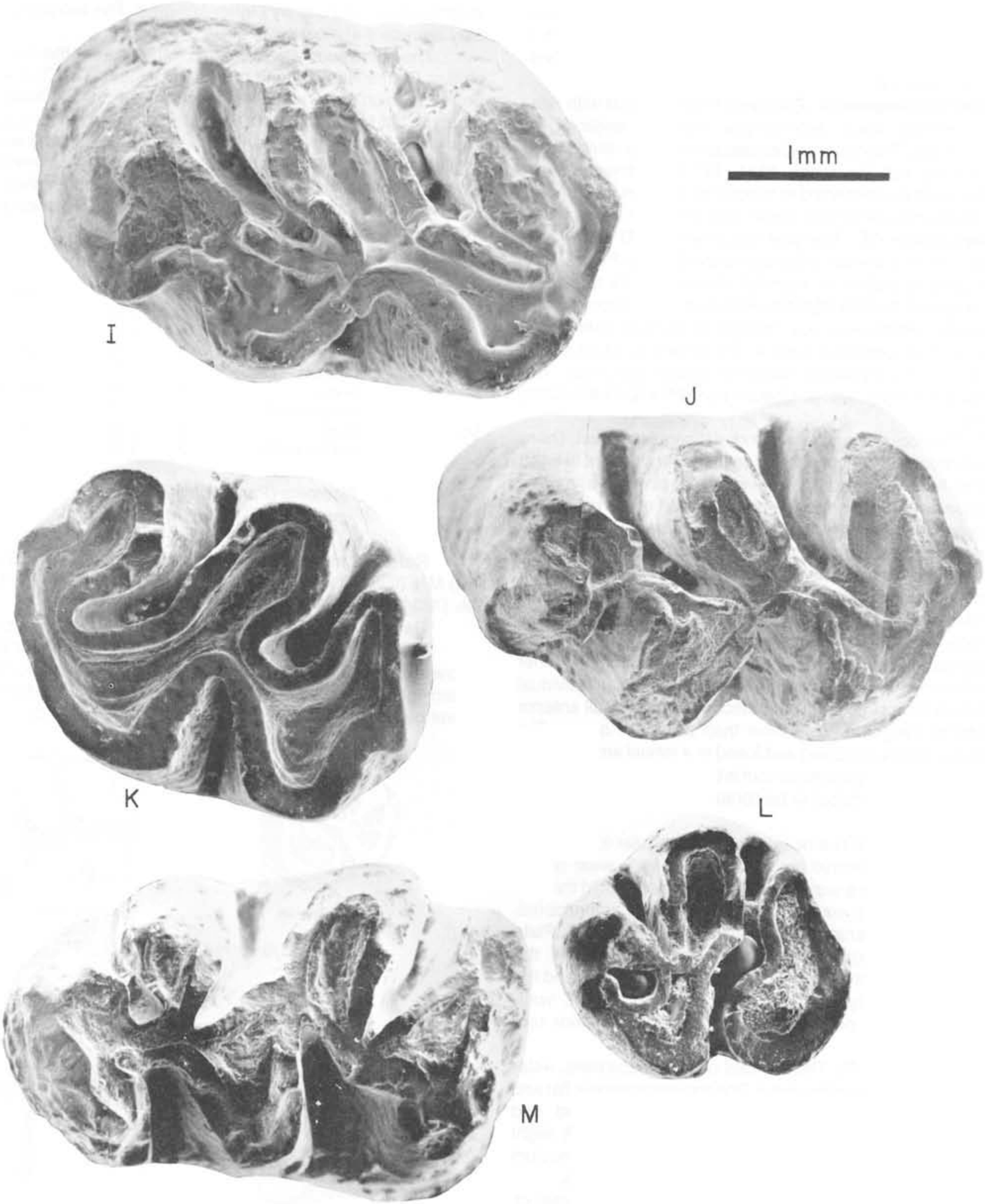


Plate 4.- Orientation as in Figure 4. A through H are all to their indicated scale, and also I through M are to their indicated scale. A—*Neotoma (Paraneotoma)* cf. *sawrockensis*, IGCU 7312, left M^2; B—*Neotoma (Paraneotoma)* cf. *sawrockensis*, IGCU 7170, right M^3; C—*Neotoma (Paraneotoma)* cf. *sawrockensis*, IGCU 7171, left M^3; D—*Neotoma (Paraneotoma)* cf. *sawrockensis*, IGCU 7172, left M^3; E—*Neotoma (Paraneotoma)* cf. *sawrockensis*, IGCU 7232, left M$_1$; F—*Neotoma (Paraneotoma)* cf. *sawrockensis*, IGCU 7233, right M$_1$; G—*Neotoma (Paraneotoma)* cf. *sawrockensis*, IGCU 7314, left M$_2$; H—*Neotoma (Paraneotoma)* cf. *sawrockensis*, IGCU 7315, right M$_2$; I—*Neotoma (Paraneotoma)* sp. indet., IGCU 7235, left M^1; J—*Neotoma (Paraneotoma)* sp. indet., EGCU 7173, left M^1; K—*Neotoma (Paraneotoma)* sp. indet., IGCU 7313, left M^2; L—*Neotoma (Paraneotoma)* sp. indet., IGCU 7381, right M^3; M—*Neotoma (Paraneotoma)* sp. indet., IGCU 7234, left M$_1$.

(Paraneotoma) spp.

Range—Sawrock Canyon, Rexroad Formation, Kansas (Hibbard, 1967); Radec, California, USGS M-1451 (unpub.); IGCU GTO 2a and GTO 2b, El Ocote, Guanajuato. Late Hemphillian and early Blancan.

Amended diagnosis—Relatively small woodrat with relatively low-crowned teeth. Anterolingual reentrant angle of M^1 poorly developed. Reentrant angles deepen near the center of the crown, but do not reach the base. M^3 trefoil-shaped, with protocone narrowly connected to hypocone. Unworn cusps blunt and rounded, occlusal surface planar with advanced wear.

Description—M^2: The one specimen (IGCU 7312) is a barely-worn tooth crowned without preserved roots (Figure 7, A, B). The occlusal outline is rounded rectangular to oval. The anterior cingulum forms a separate lobe branching buccally from the protocone, which with wear merges to form an anteroloph. Similarly, a small posterior cusp at the angled juncture of the metacone with the hypocone does not persist with wear. The anteroloph is relatively narrow. Lingual reentrant angles are poorly developed.

M^3: The occlusal outline is rounded triangular to oval. There is pronounced anterior hypsodonty, so the tooth appears to bend backwards from its roots. In little worn specimens, a narrow mediolingual bridge connects the posterior part of the protocone to the hypocone, and the posteromedial bridge connects the hypocone and metacone; these bridges become obscured with advanced wear. A small enamel lake occurs on the posteroloph between the hypocone and the posterior cingulum. Apical pits (as observed by Dalquest, 1983) occur in an unworn specimen (IGCU 7171, Plate 4, C). There are three divergent, cylindrical roots.

One barely-worn left M^3 (IGCU 7171) differs from the other two significantly, but is interpreted to be an aberrant individual rather than a distinct taxon. The metacone shows small anterior and posterior flanges, and is taller than the other cusps. The anterobuccal root is atrophied and fused to a robust anterolingual root. The resulting single anterior root is too asymmetrical, and the posterior root too cylindrical, to be confused with those of a lower molar.

M_1: The occlusal outline is elongate triangular to oval. The metaconid and anteroconid are separated in early wear (IGCU 7233, Plate 4, F); form a subequally-bilobed anterolophid through moderate wear (7231); and become a single, wide anterolophid, dominated by the anteroconid, with advanced wear (7232, Plate 4, E). The anterolingual reentrant is long and arcuate, the posterolabial reentrant wide. The posterior margin is flat, and the posteroloph relatively narrow. There are two robust, well-separated roots, the posterior root flat, and the anterior root cylindrical.

M_2 (Figure 7, E-F): The occlusal outline is quadrate, wider for its length than in living *Neotoma*. The anterior margin is flat and wide. The posterolophid becomes accentuated, widened, and arcuate with wear. The posterior margin is rounded. A slight indentation between the hypoconid and the posterior cingulum does not persist with wear. There are two robust, flat roots.

Comparisons—The type of *Neotoma (Paraneotoma)* cf. *sawrockensis* is an M^1; regrettably, there are no M^1s for this species yet known from El Ocote. Though direct comparison is still impossible, Hibbard's paratype, an M_2, is virtually identical to 7314 (Figure 7, G-H; Plate 4, G) from El Ocote.

Unpublished material from the early Blancan Radec fauna of California (Charles A. Repenning, personal communication, 1990) includes specimens of all the teeth and has been referred to *P. sawrockensis*. The Radec material is very similar to that from El Ocote, differing only in that the Radec lower molars tend to be slightly longer and slightly higher-crowned. The two populations may represent at most subspecies differences.

The holotype of *Paraneotoma minutus* from the late Hemphillian Coffee Ranch fauna of Texas (Dalquest, 1983) is an M_3, none of which have yet been recognized from El Ocote. The paratype, an M^2 (TMM 41261-47), is smaller but higher-crowned than the El Ocote material. The anteroloph is thicker and the lingual reentrant is shallower than in IGCU 7312. Reentrants extend almost to the base of the crown, not stopping short as in *P. sawrockensis* and the El Ocote teeth. *P. minutus* is quite distinct from the El Ocote woodrat.

MEASUREMENTS (in mm)

		N	X	Range
M^2	length	1	2.16	
	anterior width	1	1.72	
M^3	length	3	1.72	1.64–1.76
	anterior width	3	1.51	1.44–1.60
M_1	length	3	2.64	2.56–2.76
	posterior width	2	1.50	1.40–1.60
M_2	length	2	2.38	2.32–2.44
	anterior width	2	1.72	1.68–1.76

Neotoma (Paraneotoma) sp. indet.
(Figure 7, C, D, Figure 8; Plate 4, I-M)

Referred material—Six isolated molars, all from GTO 2a: two M^1s (IGCU 7173, 7235); one M^2 (7313); one M^3 (7381); one M_1 (7234) and an M_1 fragment (7164).

Range—GTO 2a, El Ocote, Guanajuato. Late Hemphillian.

Diagnosis—Relatively small woodrat, larger and higher-crowned than *Neotoma (Paraneotoma)* cf. *sawrockensis*. Protoloph on M^3 unconnected to posterior half of the tooth until advanced wear (Plate 4, L). Anteroconid on M_1 wide, anterior

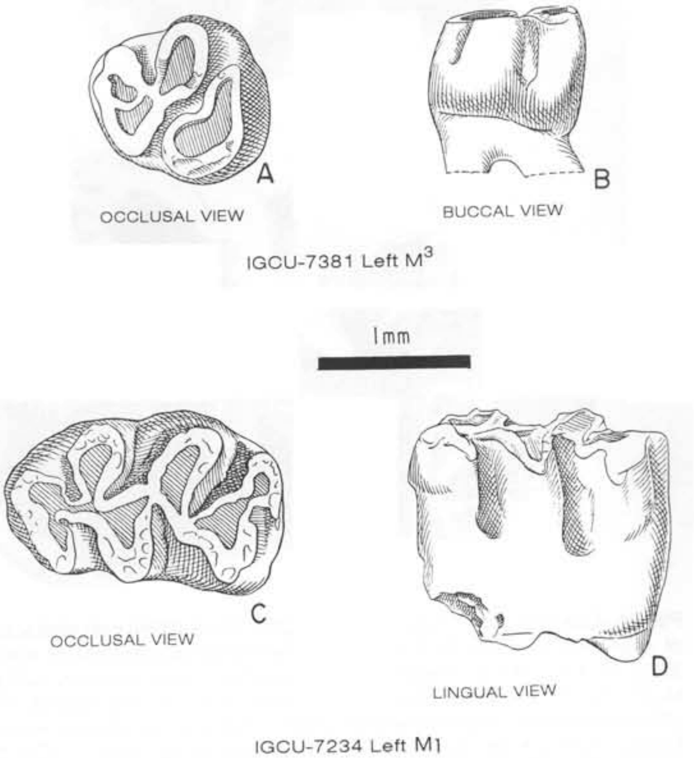


Figure 8.- *Neotoma (Paraneotoma)* sp. indet. A. IGCU 7381, left M^3, occlusal view; B. IGCU 7381, left M^3, buccal view; C. IGCU 7234, left M_1, occlusal view; D. IGCU 7234, left M_1, lingual view.

margin blunt. Lingual reentrants on lower molars deep and pronounced. Anteroconid and metaconid confluent with moderate wear. Occlusal surfaces are relatively planar even in the earliest stages of wear.

Description—M^1: Occlusal outline oval to bluntly quadrate. Anterolingual reentrant (between protocone and anterocone) deeper than in *Neotoma (Paraneotoma)* cf. *sawrockensis*. A cuspule at the junction of the hypocone and metacone effects an angled (not straight) posterior margin which persists until advanced wear. There are three roots, incompletely preserved in two specimens.

M^2 (Figure 7, C, D): Similar to the M^1 but with no anterocone, a shorter anterobuccal reentrant, and a narrower mediolingual reentrant. The occlusal outline is oval to quadrate. A cuspule at the junction of the protocone and anterior cingulum forms an angled anterior margin similar to the posterior margin. The margins become smooth and rounded with advanced wear.

There are two cylindrical buccal roots, and an elongate flat lingual root.

M^3 (Figure 8, A, B): This tooth has three transverse lophs, as in other species of *Paraneotoma*, but is not a trefoil. The posteroloph and the metacone join to form a V, which in this little to moderately worn specimen remains unconnected to the protoloph. The transverse valley is narrow and deepest at the center; with the progress of wear, a bridge to the protocone will develop, and connections will continue to expand at the margins to leave a central enamel lake with advanced wear. A small enamel lake occurs on the posteroloph between the posterior cingulum and the hypocone. There is pronounced anterior hypsodonty and three cylindrical roots.

M_1 (Figure 8, C, D): As in other species of *Paraneotoma*, but differing from *Paraneotoma* cf. *sawrockensis* in being slightly longer and especially wider in the anteroconid, which has a small but distinct labial flange. The anteroconid is apparently subequally bilobed when newly erupted, a feature immediately obliterated by wear. The anterolingual groove (between the anteroconid and metaconid) is relatively shallow. The anteroconid and metaconid become confluent with advanced wear. The lingual reentrants are particularly deep. A cuspule at the medial junction of the hypoconid and the entoconid forms a small projection into the posterolingual reentrant, which persists through moderate wear. There is a cylindrical anterior root and a flat posterior root.

Comparisons—*Neotoma (Paraneotoma)* sp. indet. probably represents a new species. However, until there is a larger or more representative sample, including M_3s, and further study of unpublished material, we hesitate to assign a formal name.

Neotoma (Paraneotoma) sp. indet. most closely resembles *Neotoma (Paraneotoma)* cf. *sawrockensis*, the smaller El Ocote woodrat described above, and the unpublished Blancan material from Radec, California, assigned by Repenning to *Paraneotoma sawrockensis* Though slightly larger, higher-crowned, and with thinner enamel than the type *P. sawrockensis* or the El Ocote *Neotoma (Paraneotoma)* cf. *sawrockensis*, *Neotoma (Paraneotoma)* sp. indet. is still not as advanced as any other species of *Neotoma*. *Paraneotoma* sp. indet. can be distinguished from *Neotoma (Paraneotoma)* cf. *sawrockensis* by the small morphological features described above.

Neotoma (Paraneotoma) sp. indet. resembles somewhat the unnamed *Neotoma* specimen reported by Miller (1980) from the Blancan Las Tunas fauna, in Baja California Sur. *Neotoma (Paraneotoma)* sp. indet. is slightly larger and less hypsodont; the Las Tunas specimen has narrower teeth and markedly shallower reentrants; nevertheless, they share some features, such as the retention of some relief with wear (primitive), the failure of reentrants to extend to the base of the crown (primitive), a relatively shallow anterolingual groove (primitive?), and a slightly wide anteroconid with a blunt, but not quadrate, anterior margin. Though their relationship is probably not much closer than their both being medium-sized primitive woodrats, *Neotoma (Paraneotoma)* sp. indet. may be more closely related to the Las Tunas specimen than any other described neotomiine species.

Remarks—Comparisons of the El Ocote woodrat material with other species are frustrated by the absence of diagnostic elements (discussed above). There are no extremely worn molars in the El Ocote sample, and most of the teeth are barely worn, so a complete wear series cannot be diagnosed, nor can enamel thickness be consistently defined. Most of the available comparative material consist of moderately to deeply worn teeth.

The larger affinities (subgenera) of neotomiines are frequently ascertained by the diagnostic M_3s—none of which are yet known from El Ocote. The recovery of M_3s for the larger *Paraneotoma* species might reveal some evolutionary direction among the species derived from primitive *P. sawrockensis*, and perhaps provides a "missing link" between *P. sawrockensis* and more advanced neotomiine species.

Both woodrat species from the late Hemphillian at El Ocote are more "primitive" (lower-crowned, thicker enamel) than the slightly older *P. minutus* from the Coffee Ranch fauna of Texas. *P. minutus* is presently the oldest known woodrat. The recovery of *Paraneotoma* from Guanajuato extends the known range of the genus southward into central Mexico.

MEASUREMENTS (in mm)

		N	X	Range
M^1	length	2	3.12	3.00–3.24
	posterior width	2	2.04	2.04–2.04
M^2	length	1	2.40	
	anterior width	1	1.80	
M^3	length	1	1.84	
	anterior width	1	1.52	
M_1	length	1	2.96	
	posterior width	1	1.80	

DISCUSSION—BIOSTRATIGRAPHY, PALEOECOLOGY

The El Ocote rodent fauna is quite similar to that of Yepómera, but there are intriguing differences. Most of them are probably ascribable to differences in environment. *Copemys* is prominent in the Yepómera fauna, but absent from El Ocote. *Copemys* immigrated to North America from Asia in the middle Miocene and maintained a north temperate range (Lindsay and Jacobs, 1985); Yepómera is its southernmost, and probably last, known occurrence.

Many of the questions raised by the El Ocote rodent fauna are ecological and taphonomic. Why are there so few worn teeth and so many unworn or barely worn teeth, many with no roots formed? Why are there no less than three species of *Prosigmodon* and three species of *Calomys* in such close association?

In comparison with other rodent faunas of late Hemphillian—early Blancan age, the El Ocote fauna is conspicuous for its diversity of cricetid rodents in combination with its southern location.

CONCLUSIONS

1. The micromammals from the two El Ocote wash sites, GTO 2a and GTO 2b, are both latest Hemphillian in age. The rodent assemblages from both sites resemble those of the Yepómera fauna.

2. The faunal association of the basal unit of Rancho El Ocote correlates with the fauna from Yepómera. Regarding what is known so far from the upper unit at El Ocote, the absence of *Teleoceras fossiger, Osteoborus cyonoides, Nannipus minor* and *Neohipparion eurystyle* suggests that the age of this unit, that contains the fauna of cricetid rodents described in this paper, could correspond to the latest Hemphillian.

3. No South American immigrants have yet been recognized among the rodent fauna. As noted by Lindsay and Jacobs (1985), this suggests the Chapadmalan age of South America should be later than early Blancan.

4. The diversity of cricetid rodents in the El Ocote fauna (four genera and at least nine and possibly as many as 11 species) is the richest so far known for any Hemphillian locality. This lends support to the hypothesis of Baskin (1978), Jacobs and Lindsay (1984) and Baskin (1986), that cricetids began their diversification in North America, specifically in the southwest and tropical Mesoamerica, prior to invading South America during the great American faunal interchange.

5. The isotopic dating of volcanic ashes has only recently been initiated at the Rancho El Ocote. The future application of paleomagnetic methods to the El Ocote section is eagerly anticipated. Work in progress on the other micromammals from El Ocote and on other Hemphillian-Blancan localities in Guanajuato will potentially shed light on an important evolutionary arena.

ACKNOWLEDGMENTS

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