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Geology and mammalian paleontology of the Horned Toad Hills, Mojave Desert, California, USA

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ABSTRACT

The Horned Toad Formation includes five lithostratigraphic members that record alluvial fan, fluvial, lake margin, and lacustrine deposition within a relatively small basin just south of the active Garlock fault during the late Miocene to early Pliocene. These sediments experienced northwest-southeast contractional deformation during the Pliocene-Pleistocene associated with basement-involved reverse faults. Member Two of the Horned Toad Formation has vielded 24 taxa of fossil mammals, referred to as the Warren Local Fauna, including Cryptotis sp., cf. Scapanus, Hypolagus vetus, Hypolagus edensis, ?Spermophilus sp., Prothomomys warrenensis n. gen., n. sp., Perognathus sp., Repomys gustelyi, Postcopemys valensis, Peromyscus sp. A, Peromyscus sp. B, Jacobsomys dailyi n. sp., Borophagus cf. B. secundus, cf. Agriotherium, Machairodus sp. cf. M. coloradensis, Rhynchotherium sp. cf. R. edensis, Pliomastodon vexillarius, Dinohippus edensis, Teleoceras sp. cf. T. fossiger, cf. Prosthennops, Megatylopus sp. cf. M. matthewi, Hemiauchenia vera, Camelidae gen. et. sp. indet., and the antilocaprid cf. Sphenophalos. The majority of fossil localities are confined to a 20 m thick stratigraphic interval within a reversed polarity magnetozone. The fauna demonstrates affinity with other late Hemphillian faunas from California, Nevada, Nebraska, Texas, and Mexico. The Lawlor Tuff, dated elsewhere in California at 4.83 ± 0.04 Ma and geochemically identified in the Horned Toad Formation, overlies most of the fossil mammal localities. Magnetic polarity data are correlated with Chrons 3n.3r, 3n.3n, and 3n.2r, suggesting an age of approximately 5.0 - 4.6 Ma. These constraints indicate an age for the late Hemphillian Warren Local Fauna of 4.85 - 5.0 Ma.

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INTRODUCTION

The Horned Toad Hills are located along the northwestern margin of the Mojave Desert, California, where 430 m of nonmarine sediments are exposed in low hills just south of the Garlock fault, northwest of the town of Mojave, Kern County, California. The definition of the Horned Toad Formation is extended to include the original three members described by Dibblee (1958) and two new members. The late Miocene to early Pliocene sediments of the Horned Toad Formation were deposited in fluvial and lacustrine environments on an erosional terrain of Cretaceous granitic and Miocene volcanic rocks. Based on analyses of clast composition, the sediments of the Horned Toad Formation were derived locally. A volcanic tuff in the Horned Toad Formation has been geochemically identified as the Lawlor Tuff that has been dated elsewhere at 4.83 ± 0.04 Ma (McLaughlin et al. 2005; Sarna-Wojcicki et al. 2005b).

The Horned Toad Formation is deformed into open folds associated with basement-involved reverse faults. Major structural features trend northeast-southwest, roughly parallel to the trace of the Garlock fault that is located just north of the Horned Toad Hills. Structural deformation of the granitic basement and overlying sediments within the Horned Toad Hills may be related to post-5 Ma movement on the Garlock fault or to regional northsouth compressional deformation in the Mojave Desert (Bartley et al. 1990). The deformed Horned Toad Formation is unconformably overlain by alluvium of Pleistocene (?) to Quaternary age.

Fossil mammals from the Horned Toad Formation include the following taxa: *Cryptotis sp.*, cf. *Scapanus*, *Hypolagus vetus*, *Hypolagus edensis*, ?Spermophilus sp., *Prothomomys warrenensis* n. gen., n. sp., *Perognathus* sp., *Repomys gustelyi*, *Postcopemys valensis*, *Peromyscus* sp. A, *Peromyscus* sp. B, *Jacobsomys dailyi* n. sp., *Borophagus* cf. *B. secundus*, cf. *Agriotherium*, *Machairodus* sp. cf. *M. coloradensis*, *Rhynchotherium* sp. cf. *R. edensis*, *Pliomastodon vexillarius*, *Dinohippus edensis*, *Teleoceras* sp. cf. *T. fossiger*, cf. *Pros-* thennops, Megatylopus sp. cf. M. matthewi, Hemiauchenia vera, Camelidae gen. et. sp. indet., and cf. Sphenophalos. The majority of fossil localities are confined to a 20 m thick stratigraphic interval within Member Two of the Horned Toad Formation, although limited fossils have also been collected from higher in the stratigraphic sequence in Members Three and Four.

Fossil mammals from below the Lawlor Tuff are placed in the Warren Local Fauna. Based on taxonomic composition and stage of evolution, the Warren Local Fauna is latest Hemphillian in age (Hh4; Tedford et al. 2004) and shows affinities with faunas from California, the southern Great Basin, and Mexico. Tephrochronology and magnetic polarity stratigraphy suggest correlation of the Warren Local Fauna with Chron 3n.3r or 4.896 – 4.997 Ma following the time scale of Lourens et al. (2004). Fossil mammals from Members Three and Four of the Horned Toad Formation are from a younger reversed polarity magnetozone that is correlated with Chron 3n.2r or 4.631 - 4.799 Ma. The stratigraphically lowest normal polarity site in the intervening normal polarity magnetozone is from the Lawlor Tuff (4.83 ± 0.04 Ma). Fossils found above the Lawlor Tuff include Jacobsomys dailyi n. sp. and *Dinohippus edensis*, and may be early Blancan in age, although no definitive Blancan taxa have yet been identified from this stratigraphic interval. The interpreted age of the Warren Local Fauna (4.85 – 5.0 Ma) is consistent with an age for the Hemphillian-Blancan land mammal age boundary of approximately 4.8 - 4.9 Ma (Lindsay et al. 2002).

GEOLOGIC SETTING

The Horned Toad Hills are located in the northwestern edge of the Mojave Desert geologic province (Figure 1). The Garlock fault, which forms the northern boundary of this province, lies just north of the Horned Toad Hills and is interpreted as a transform structure that separates a domain of large-scale late Cenozoic extension on the north from more limited Cenozoic extension to the south



FIGURE 1. Location of the Horned Toad Hills in the northwestern Mojave Desert, southern California.

in the Mojave Desert (Davis and Burchfiel 1973; Christiansen and Yeats 1992). Evaluation of regional kinematic indicators in the western U.S. by Hearn and Humphreys (1998) agrees with earlier interpretations (Davis and Burchfiel 1973) that the Garlock fault accommodates the western dilation of the Great Basin and the northwest motion of the Sierra Nevada relative to the Mojave block.

Sixty-four km of left-lateral displacement have been documented across the Garlock fault (Smith 1962). Smith et al. (2002) presented evidence for 32-40 km of displacement since approximately 10 Ma and suggested initiation of motion at approximately 16 Ma based on an assumption of constant slip rate. On the basis of correlative volcanic units north and south of the Garlock fault, Monastero et al. (1997) interpreted initiation of movement after 17 Ma, generally consistent with the initiation of major extension in the Death Valley system and supports a kinematic linkage. Burbank and Whistler (1987) and Loomis and Burbank (1988) have suggested a younger age (9-10 Ma) for initiation of slip on the Garlock fault. The average slip rate calculated by Smith et al. (2002) (3.1-3.8 mm/yr) is about half that estimated by McGill and Sieh (1993) for the Holocene (6-8 mm/yr) and by Carter (1987) for the Pleistocene (7 mm/yr). Regardless of whether slip initiated in the early or middle Miocene, the Garlock fault was an active, left-lateral strike-slip fault during the deposition of the Horned

Toad Formation. No offset equivalent of the Horned Toad Formation has been identified north of the Garlock fault. Facies relationships and sediment provenance suggest that the Horned Toad Formation was deposited in a localized basin.

The western Mojave Desert province includes Neogene sedimentary basins separated by low hills of Mesozoic granitic rocks, Tertiary volcanic and volcaniclastic rocks, and older metamorphosed sedimentary rocks. Neogene deformation of the Mojave block has been associated with crustal extension, strike-slip deformation, block rotation, and north-south compression. Dokka (1989) recognized a number of structural domains within what he termed the Mojave Extensional Belt that reflect differing amounts and geometries of extension during the early Miocene. Since about 20 Ma, the western Mojave has been deformed along a series of sub-parallel, northwest trending right-lateral strike-slip faults with cumulative displacement of up to 40 km (Dokka 1983). Kamerling and Luyendyk (1979), Hornafius et al. (1986), Golombeck and Brown (1988), Ross et. al., (1989), MacFadden et. al., (1990a, 1990b), Ross (1995), Dokka and Ross (1995) and others have presented paleomagnetic evidence for both clockwise and counterclockwise rotation of fault-bounded crustal blocks in the Mojave during the Neogene. Kanter and McWilliams (1982) and Plescia and Calderone (1986) have presented evidence for clockwise rota-



FIGURE 2. Aerial view looking north of the Horned Toad Hills (Th = Horned Toad Formation), Cameron Ridge (CR), and southern Sierra Nevada (SN). The Garlock fault lies between Cameron Ridge and the Sierra Nevada.

tion of the Tehachapi Mountains north of the Horned Toad Hills between about 80 and 20 Ma.

Mesozoic plutonic rocks represent the most common pre-Cenozoic lithologies in the vicinity of the Horned Toad Hills. The most important of these is the Cretaceous Cameron Granodiorite that forms the northeast-southwest trending Cameron Ridge, upon which the sediments of the Horned Toad Formation were deposited (Figures 2 and 3) (Ross 1980). Ross (1989), who referred to this unit as the "Granodiorite of Cameron," differentiated it from other granitoid units in the area with similar modal mineralogy by its coarse-grained texture, twinned feldspars, and striking salmon-pink K-feldspars at some outcrops. The Cameron Granodiorite is bounded on the north by the Garlock fault and was an important source terrain for sediments of the Horned Toad Formation.

Late Oligocene to Miocene volcanic and sedimentary rocks have been mapped at Soledad Mountain and in the Rosamond Hills south of the Horned Toad Hills. Dibblee (1958) included the rocks exposed in the Rosamond Hills in the Tropico Group as a sequence of non-marine sediments and volcanic rocks overlying Cretaceous plutonic basement. The Tropico Group was subdivided by Dibblee into the Gem Hill Formation, the Fiss Fanglomerate, and the Bissell Formation. Dibblee (1963) described the early Miocene Gem Hill Formation as a stratified sequence of rhyolitic, lithic and lapilli tuffs, and tuff breccias with local facies of tuffaceous conglomeratic sandstone, volcanic conglomerate and siliceous shale, chert and limestone. The pyroclastic material of the Gem Hill Formation was derived from vents in the Soledad Mountain area that are now preserved as plugs of Bobtail Quartz Latite (Dibblee 1963). Bobtail Quartz Latite is also exposed in the western Horned Toad Hills where it apparently intrudes the Cameron Granodiorite and is overlain by sediments of the Horned Toad Formation (Member One) (Figure 4). Clasts of the Bobtail Quartz Latite



FIGURE 3. Geologic map of the Horned Toad Hills.



FIGURE 4. Geologic map and cross section in the western Horned Toad Hills illustrating relationship of Member One of the Horned Toad Formation with basement rocks of the Miocene Bobtail Quartz Latite and the Cretaceous Cameron granodiorite.

are easily recognized in the coarser sediments of the Horned Toad Formation.

HORNED TOAD FORMATION

The Horned Toad Formation is exposed entirely within the Horned Toad Hills northwest of Mojave, California (Figures 2 and 3). The formation was named by Dibblee (1958) who proposed a threefold division into lower, middle, and upper members. These three members, as well as two new members, are recognized in the present study. Dibblee (1959) published a "Preliminary Geologic Map of the Mojave Quadrangle" that included most of the Horned Toad Formation. A portion of this map, along with new data from the Tehachapi Quadrangle, was published by Dibblee (1967). The Horned Toad Formation consists primarily of arkosic sandstone and conglomeratic sandstone along with siltstone, clay, and rare volcanic tuff and chert. It is here subdivided into five lithologic members (Figures 3 and 5).

Lithostratigraphy

Member One – The basal member of the Horned Toad Formation is equivalent to Dibblee's (1958) "Lower Member". This member has a maximum thickness of 297 m and is exposed for 9.5 km along the southeast flank of Cameron Ridge (Figure 3). The lower contact of Member One is a depositional nonconformity on Cameron Granodiorite and Bobtail Quartz Latite (Figures 4 and 5). Bedding attitudes near the contact are generally steep, but there is little evidence for structural deformation at the sediment-basement interface. Therefore, the basement has also been tilted to the southeast. A basal conglomerate, up to a few meters thick is present locally and contains rounded to wellrounded, boulder size clasts, up to 3 m in diameter, of both volcanic and granitic lithologies similar to the local basement (Figure 6). Where the basal conglomerate is absent, it is often difficult to identify the basement contact because the grus developed on the Cameron Granodiorite is very similar to sandstones of Member One.

Member One is primarily composed of poorly sorted, poorly to moderately indurated, arkosic sandstone and conglomeratic sandstone. The color of these sediments ranges from gray-tan to reddish-brown depending on the amount of muddy matrix present. Bedding is generally thick, massive, laterally variable, and commonly defined by variability in abundance of pebble-to-cobble size clasts (Figures 7 and 8). Normally graded beds and trough cross-beds are present locally. Granitic and silicic volcanic clasts are subangular to rounded, pebble to boulder size, and clearly were derived from the nearby Cameron Granodiorite and the Bobtail Quartz Latite. Well-rounded, pebble-to-cobble size clasts of gneiss are very rare. The upper part of Member One fines upward and becomes dominated by tan to brown sandstones and siltstones.

Member Two – Member Two rests conformably on Member One and is equivalent to Dibblee's (1958) "Middle Member". The lower contact is marked by a distinct color change from tans and browns below to light grays and white above. In detail, this contact is often gradational over a few meters with thin, gray, calcareous siltstone layers characteristic of Member Two interbedded with brown silt and sandy silt at the top of Member One (Figure 9). Member Two is the most distinctive member of the Horned Toad Formation because of its relatively resistant nature and its light gray to white color (Figure 10). The outcrop pattern clearly defines the primary structural geometry of the Horned Toad



FIGURE 5. Measured stratigraphic sections in the Horned Toad Hills. Locations shown on inset map. Lithostratigraphic correlations shown by black dashed lines; correlation of Lawlor Tuff shown in red dashed line.

Hills. Fossil mammals representing the Warren Local Fauna were collected primarily from Member Two.

Member Two ranges in thickness from a few meters to a maximum of approximately 25 m (Figure 5). It thins to the southwest and to the northeast. Member Two consists of light gray to white, moderately to well indurated calcareous siltstone, sandy siltstone, sandstone, volcanic tuff, and chert. Thin to thick bedding is distinct, and sedimentary structures include cross-bedding and ripples (Figure 11). The light color of Member Two is the result of abundant carbonate, both as cement and as a primary component of some beds. At least two tuffs are present in Member Two, a lower andesitic tuff that is discontinuous in extent and an upper silicic tuff referred to as the "marker tuff" by May (1981a) that is more continuous, and has been identified geochemically as the Lawlor Tuff (see discussion below). The "marker tuff" is a 20-40 cm thick, water-lain, airfall deposit composed primarily of glass shards (Figure 12). A secondary detrital component includes rounded quartz grains and a diverse heavy mineral assemblage, including rounded zircons. In the western and central outcrop areas, the "marker tuff" occurs near the top of Member Two; it climbs stratigraphically to the northwest and is present within the green mud-



FIGURE 6. Boulder size clast of Bobtail Quartz Latite in Member One of the Horned Toad Formation. Rock hammer for scale.

stones of Member Three on the north limb of the Warren syncline (Figure 5).

Recognition of the Lawlor Tuff is important to our age interpretation of the Horned Toad Formation and the Warren Local Fauna. The "marker tuff" was identified as the Lawlor Tuff on the basis of the chemical composition of the volcanic glass (sample HTH-1; A.M. Sarna-Wojcicki, written communication to C. Repenning and S. May 1982). The Lawlor Tuff is a widespread Pliocene tephra layer that was erupted from the Sonoma Volcanics in the central Coast Ranges of California (Sarna-Wojcicki



FIGURE 7. Coarse arkosic sandstone of Member One. Bedding is defined by alignment of cobble size clasts. Rock hammer for scale.

1971, 1976; Sarna-Wojcicki et al. 1979). A K-Ar age of ~ 4.0 \pm 0.2 Ma, obtained on plagioclase crystals separated from the Lawlor Tuff (Sarna-Wojcicki 1976), was later revised to 4.1 Ma after revision of the 40 K decay constant by Steiger and



FIGURE 8. Tan to brown, arkosic sandstone of Member One. Bedding is defined by slightly better cemented pebbly sandstone (PS). Rock hammer for scale to the right of (PS).



FIGURE 9. A locally gradational contact between Members One and Two is evidenced by thin beds of white, calcareous siltstone characteristic of Member Two, interbedded with brown sandy siltstone at the top of Member One. Rock hammer for scale.

Jäger (1977). The Lawlor Tuff was redated in 1994 by A. Deino of the Berkeley Geochronology Center using the 40 Ar/ 39 Ar laser-fusion step-heating technique (McLaughlin et al. 2005), and an age of 4.83 \pm 0.04 Ma was obtained on multiple individual plagioclase crystals. In the Tassajara Hills, in the central Coast Ranges of California, the Lawlor Tuff is overlain by the Huichica Tuff (4.71 \pm 0.03 Ma) (McLaughlin et al. 2005).

In 2006, the original geochemical data from the "marker tuff" were reexamined and additional samples were collected to test the correlation with the Lawlor Tuff. The original sample, HTH-1, collected from the western part of the mapped area, was supplemented by HTH-4, from the central part,



FIGURE 10. Typical exposures of Member Two looking north toward Cameron Ridge with the peaks of the southern Sierra Nevada on the right skyline. The majority of fossils from the Horned Toad Hills have been collected from these sediments that represent fluvial to lake margin depositional environments.



FIGURE 11. Cross-bedded fluvial sandstone (at rock hammer) overlies a sandy mudstone that was probably deposited as a mudflow. The *Rhynchotherium* cf. *R. edensis* skeleton was collected from lower mudstone interval (RV-6834).

and HTH-5, from the eastern part of the area on the north limb of the Warren syncline. In addition, samples of a second tuff, located 14 m stratigraphically below the "marker tuff" (HTH-2 and HTH-3), were collected from the western part of the study area.

Samples HTH-4 and HTH-5 of the "marker tuff", and sample HTH-3 of the underlying tuff from the western part of the study area, were analyzed and their chemical compositions determined. A JEOL 8600 electron microprobe was used to analyze volcanic glass shards separated from the tuffs for nine major and minor elements, which are presented in Table 1, as oxides: SiO₂, Al₂O₃, Fe₂O₃,



FIGURE 12. Exposure of Lawlor Tuff near top of Member Two. Rock hammer for scale.

TABLE 1. Comparison of the chemical composition of glass of the Marker Tuff Bed in the Horned Toad Hills with that of the 4.83-Ma Lawlor Tuff (type locality) in the San Francisco Bay area. Analysis by elecron microprobe (JEOL 8600), at the U.S. Geological Survey, Menlo Park, Calif. Charles Meyer, James Walker, David Wahl, and Elmira Wan, analysts (1982-2006). Analyses recalculated to a 100% fluid-free base to compensate for differences in hydration of glass. Sample HTH-5, obtained from Member 3, playa sediments, may be partly leached of Fe_2O_3 . Composition of the tephra layer underlying the Marker Tuff Bed, HTH-3, is shown for comparison.

	SiO2	AI2O3	Fe2O3	MgO	MnO	CaO	TiO2	Na2O	K2O	Total,R
Marker Tuff Bed at Hor	ned Toad	Hills, Mojav	ve Desert (⊢	ITH-1, wes	stern part	of study a	rea; HTH-4	1, central pa	irt; HTH-5, e	astern part)
HTH-1, T43-2	73.41	14.46	2.15	0.08	0.05	0.84	0.17	5.05	3.78	99.99
HTH-4, T546-2	74.02	14.19	2.11	0.10	0.04	0.85	0.19	4.62	3.88	100.00
HTH-5, T546-3	74.08	14.20	1.99	0.09	0.04	0.88	0.17	4.93	3.63	100.01
Lawlor Tuff, type localit ash-flow tuff	y in Lawlo	r Ravine, Lo	os Medanos	Hills, eas	tern San I	Francisco	Bay area. I	_AWLOR-1,	fall pumice;	LAWLOR-2,
LAWLOR-1 T325-9	73.20	14.29	2.15	0.09	0.04	0.84	0.18	4.83	4.37	99.99
LAWLOR-1 T530-7	73.78	14.07	2.13	0.10	0.05	0.85	0.18	4.66	4.19	100.01
LAWLOR-2 T325-10	73.10	14.32	2.21	0.10	0.04	0.86	0.17	4.79	4.41	100.00
Statistics for the Lawlor	r Tuff, ash	/pumice fall	and ash-flo	w, from 43	B localities	s in Califor	nia, Nevac	la, and Arizo	ona	
Lawlor Tuff, Mean, 43 samples	73.79	14.23	2.16	0.10	0.04	0.88	0.17	4.44	4.18	100.00
Standard Deviation (±1σ)	0.61	0.27	0.05	0.01	0.01	0.03	0.01	0.46	0.53	0.01
Range	2.83	1.32	0.24	0.04	0.05	0.12	0.06	2.38	3.01	0.04
Minimum	72.95	13.49	2.03	0.08	0.02	0.83	0.14	2.98	2.29	99.98
Maximum	75.78	14.81	2.27	0.12	0.07	0.95	0.20	5.36	5.30	100.02
Tephra Layer HTH-3, u	Tephra Layer HTH-3, underlying the Marker tuff Bed with ~14 m separation, at the Horned Toad Hills									
HTH-3, T546-1 (all shards)	64.75	15.42	5.68	1.65	0.09	3.94	1.00	4.15	3.32	100.00
HTH-3, T546-1 (high Ca, Fe)	61.65	16.05	6.95	2.30	0.10	5.00	1.07	4.15	2.74	100.01
HTH-3, T546-1 (med, Ca, Fe)	65.94	15.08	5.21	1.37	0.08	3.55	1.00	4.22	3.56	100.01
HTH-3, T546-1 (low Ca, Fe)	69.19	14.77	3.82	0.82	0.07	2.38	0.87	3.96	4.12	100.00
MSE 202 (1) T75-1	65.53	15.17	5.34	1.57	0.13	3.83	0.99	3.86	3.59	100.01
TWN-L-2.235B	66.00	15.48	5.05	1.49	ND	4.02	1.04	4.19	2.72	99.99
T2023M.12MTB;2, T187-2	65.15	16.06	5.11	1.70	0.09	3.93	0.93	4.40	2.63	100.00
Samples of the Pinole	Tuff, easte	ern San Fra	ncisco Bay	area						
758-190B, T1-7, P	63.55	16.15	6.98	1.07	0.15	3.27	0.92	6.13	1.97	100.01
758-181A. T1-9. P	61.57	16.36	5.32	2.27	0.09	4.60	0.96	4.11	4.71	99.99
758-178B, T1-13. P	71.27	14.39	3.56	0.09	0.08	1.09	0.23	5.79	3.49	99.99

MgO, MnO, CaO, TiO₂, Na₂O, and K₂O. The glass shards were separated and cleaned by physical and chemical methods. Relevant laboratory procedures, analytical conditions, and data evaluation techniques used are given in Sarna-Wojcicki et al. (1984, 2005a) and Sarna-Wojcicki (2000).

Results of the chemical analysis indicate that samples of the "marker tuff" (HTH-4 and HTH-5) match the previously analyzed HTH-1, as well as the Lawlor Tuff (Table 1; Figure 13). The analyzed samples were compared with over 5600 analyses of tephra samples contained in the U.S. Geological Survey's database of Upper Neogene samples collected from the western USA, Alaska, and Mexico. These data are stored at the U.S. Geological Survey's Tephrochronology Laboratory in Menlo Park, California. Samples HTH-1, 4, and 5 all match, at high similarity coefficients, with samples from the Lawlor Tuff collected at its type locality in Lawlor Ravine, in the Los Medanos Hills, in the eastern



FIGURE 13. Results of CaO vs. FeO analysis for volcanic glass from the "marker tuff" in the Horned Toad Formation (H4, H5) and the Lawlor Tuff from its type locality in the San Francisco Bay area (LAWLOR 1A, LAWLOR-1B, LAW-LOR-2). H-5 is more hydrated and may be partially leached. Values plotted are initial values on analysis, not recalculated to 100% fluid-free basis.

San Francisco Bay area. Sample LAWLOR-1 is the pumice fall deposit, and LAWLOR-2, the overlying ash-flow unit. Similarity coefficients are also high when samples HTH-1, 4, and 5 are compared to the average of 43 analyses of well documented samples of the Lawlor Tuff collected from other locations in California, Nevada, and Arizona (Figure 14). Similarity coefficients are well within the range determined for replicate analysis of samples obtained from a single tephra layer. We note that values for sodium and potassium are scattered, an observation that applies to other tephra layers we have analyzed, particularly for older tephra layers, where different parts of the same layer were deposited under different depositional environments, or buried and stored under different climatic or geochemical conditions. For sample, in HTH-5, the iron values are somewhat lower than for most samples of the Lawlor Tuff, and we suspect that some leaching of iron from the glass, as well as hydration and alkali mobility, may have occurred.

A second tuff was identified and collected during a visit to the Horned Toad Hills in 2006 (HTH-3 in Table 1). This tuff is darker in color and is discon-



FIGURE 14. Map of western U.S. showing localities where Lawlor Tuff has been geochemically identified. Red dot in the northwestern Mojave Desert is the Horned Toad Hills.

tinuous giving the appearance that it was preserved in local depositional depressions. It is preserved immediately above the most prolific fossil mammal locality in the Horned Toad Formation (RV-7702), where it thickens up to 30-40 cm (Figure 15). This tuff appears to be more andesitic in composition than the Lawlor Tuff, and geochemical results do not match any of the samples in the U.S.G.S. database. It is most similar to a group of andesitic tephra layers erupted from the Cascade Range-for example, samples MSE 202, TWN-L-2.235B, and T2023M.12MYB;2,T187-2 (Table 1). These three samples are derived from the Cascade Range; from Mount Adams, Washington, Tawny Lake, Oregon, and Tule Lake, in northwestern California, respectively. However, all are late Pleistocene and Holocene in age, too young to match the tuff of sample HTH-3. Geochemical identification of the lower tuff in Member Two of the Horned Toad Formation awaits further study.

Member Three – This member corresponds to the "Upper Member" of Dibblee (1958, 1959, 1967) and consists primarily of greenish mudstone, clay, and silty clay. Member Three is exposed on both



FIGURE 15. Typical outcrop of Member Two with light gray to buff siltstone, sandstone and volcanic tuffs. Line drawing below shows the Lawlor Tuff (red dashed line), the lower discontinuous tuff (darker gray) and the sandy siltstone interval in buff that yielded the prolific fossil mammal locality (RV-7702). Rock hammer for scale.



FIGURE 16. Sharp depositional contact between light gray siltstone and sandy siltstone of Member Two (Th2) and the greenish, bentonitic clay of Member Three (Th3). Resistant bed near the top of Member Two is the Lawlor Tuff. Five foot Jacob's staff above backpack for scale.

limbs of the Warren syncline, but thins and eventually pinches out to the southwest in Section 35 (T12N, R13 W, SBBM) (Figures 3 and 5). The maximum measured thickness is approximately 30 m. Where present, the greenish mudstones of Member Three rest conformably on the light gray to white siltstone and sandy siltstone of Member Two (Figure 16). The upper part of Member Two and the lower part of Member Three are laterally equivalent facies based on their relationship to the Lawlor Tuff (Figure 5). Member Three mudstones weather with a characteristic "popcorn" texture and bedding is indistinct in most outcrops (Figure 17).

Member Four – Inclusion of the brown silts and sands of Member Four within the Horned Toad Formation extends the concept of this formation beyond that originally proposed by Dibblee (1958).



FIGURE 17. View to the northeast along the south limb of the Warren syncline illustrating the conformable nature of Members Two (Th2), Three (Th3), and Four (Th4) (top of the hill) dipping to the northwest. At this and other localities, Member Four is clearly conformable with the underlying strata.



FIGURE 18. 1. Sharp, structurally conformable contact of Member Four (Th4) on Member Three (Th3). At this locality, the base of Member Four is a thick channelform sandstone that rests on greenish-brown clays and calcareous claystone of Member Three. 2. Close up of contact above showing convex-up dish structures in Member Three calcareous claystone beds. These structures are interpreted as dewatering structures probably associated with rapid burial by the Member Four channel sand. Rock hammer for scale.

Dibblee recognized this lithostratigraphic unit, but considered it to lie unconformably on the Horned Toad Formation and included it in Pleistocene Older Alluvium. Numerous lines of evidence indicate that Member Four is conformable with the underlying units and should be included in the Horned Toad Formation.

The areal extent of Member Four is consistent with the underlying members as are bedding attitudes (Figures 3 and 17). Dibblee (1967) illustrated an angular discordance between his "sand and silt" unit (= Member Four) and the underlying members of the Horned Toad Formation. He mapped this relationship in the north half of Section 36 (T12N, R13W, SBBM). Remapping of this area (Figure 3) reveals that the contact, previously interpreted as an unconformity, is a fault that places southeasterly dipping strata of Member Four against northwesterly dipping sediments of Member Three.

The Member Three – Member Four contact is often a gradational color change from green to greenish-brown to brown, accompanied by an increase in the amount of silt and fine sand (Figure 17). Figure 18 shows an outcrop in which the contact between Members Three and Four is well



FIGURE 19. Poorly sorted, sandy conglomerate within Member Five. Pebble to small boulder size clasts are dominated by subrounded to angular Bobtail Quartz Latite lithologies. Rock hammer for scale.

exposed. At this locality, the base of Member Four is a lenticular channel deposit of fine to very coarse sand approximately 2-3 m thick with internal trough cross bedding and normal graded bedding. The base of this channelform sandstone is a sharp contact with underlying greenish-brown clays of Member Three. These clays exhibit soft sediment deformation features including contorted laminations and convex-up dish structures (Figure 18.2). These features probably were produced by the rapid loading of heavy channel sands on the watersaturated clays. At the margins of the channelform sandstone, the clays of Member Three interfinger with the sand on a very small scale. These relationships document the depositional conformity of Member Four on Member Three and their relative proximity in age.

Member Four initiates a coarsening upward trend in the Horned Toad Formation with lithologies ranging from silty clay, siltstone, and sandstone at the base to sandstone and pebbly sandstone farther up section. These sediments are poorly indurated, and bedding is generally poorly defined except for thin, indurated beds of coarse sandstone and conglomeratic sandstone. These conglomeratic units of Member Four contain abundant silicic volcanic clasts and lesser amounts of granitic clasts.

Member Five – As with Member Four, Member Five is a stratigraphic extension of the Horned Toad Formation. Dibblee (1967) recognized and mapped this lithologic unit, but considered it to belong to Pleistocene Older Alluvium. Our mapping indicates that Member Five lies conformably on Member Four with a gradational contact recognized by an increase in pebble-to-boulder size



FIGURE 20. Exposure on the north limb of the Warren syncline showing Members Two (Th2) and Three (Th3) dipping to the right (southeast) overlain unconformably by unconsolidated sands assigned to Older Alluvium (OA).

clasts. Member Five is exposed in the axis of the Warren syncline and along the southeastern edge of the Horned Toad Formation. It has a maximum measured thickness of 90 m and is unconformably overlain by Older Alluvium. Member Five continues the upward coarsening trend established in Member Four. Dominant lithologies include poorly indurated, tan to brown conglomeratic sandstone with indistinct bedding defined by relative clast abundance and rare well-cemented sandstone lenses. Member Five is similar to Member One with poorly sorted arkosic sand matrix and pebble-to-boulder size clasts (Figure 19). However, unlike Member One, 75-85% of the clasts are silicic volcanic lithologies and 15-25% granitoid. This proportion suggests that the Cameron Granodiorite was less important as a source terrain while the volcanic rocks of the Tropico Group (including the Bobtail Quartz Latite) were still providing detritus to the Horned Toad basin.

All five members of the Horned Toad Formation are unconformably overlain by unconsolidated sands and gravels assigned to "Older Alluvium" (Figures 3 and 20). The Older Alluvium defines a remnant surface that has been erosionally dissected by washes that carry Quaternary alluvium (Figure 21).

Depositional Environments

The Horned Toad Formation is a nonmarine sequence of fluvial and lacustrine sediments deposited on a basement of Cretaceous Cameron Granodiorite and Miocene Gem Hill Formation (Bobtail Quartz Latitie). Members One through Three record a generally fining upward trend followed by a coarsening upward trend in Members Four and Five. Provenance reconstruction of the clast types in Members One, Four, and Five indi-



FIGURE 21. In the western portion of the Horned Toad Hills, fans of Older Alluvium (OA) are less dissected and slope gently from Cameron Ridge toward the southeast.

cate local source terrains to the northwest (Cameron Granodiorite) and south (Gem Hill Formation). Volcanic clasts in the Horned Toad Formation are petrographically indistinguishable from rocks to the southwest and south that are included in the Bobtail Quartz Latite member of the Gem Hill Formation. Granitic clasts can be divided compositionally into granodiorites and granites. Petrographically, these lithologies are very similar mineralogically and texturally to the Cameron Granodiorite (Ross 1989). Sediments of the Horned Toad Formation appear to have been derived locally and can be correlated with source terrains south of the Garlock fault.

The interbedded sandstones and mudstones of Member Two are interpreted as fluvial to lacustrine depositional facies associated with a playa or lakeshore environment that received occasional muddy debris flows at the distal toes of alluvial fans. Channelform, sandy facies with trough crossbedding and normal grading are interpreted as stream-channel deposits, while lake-plain to lacustrine facies are represented by calcareous siltstones and mudstones. Fossils recovered from Member Two include pond turtle, frog, duck, ostracodes, and diatoms. J.P. Bradbury and R.M. Forester (personal commun., 1981) interpreted the microfossils to reflect near-shore, marshy conditions. Slender root casts are also preserved in siltstones of Member Two. Thin silt and claystone beds, the Lawlor Tuff, and rare cherts were deposited in standing water. Locally, the Lawlor Tuff is stratified with a lower massive interval dominated by glass shards and interpreted as the primary airfall deposit. This is overlain by thinly bedded tuff with local normal grading and an increased abundance of detrital material.

The greenish clays of Member Three record the presence of a permanent lake. As described above and shown in Figure 5, the Lawlor Tuff is associated with the top of Member Two in the central outcrop area, but climbs stratigraphically into Member Three to the northeast. This indicates that lake margin facies of Member Two are temporally equivalent to the lacustrine facies of Member Three. The facts that the Lawlor Tuff climbs approximately 15 m stratigraphically in less than one mile and that the lacustrine facies of Member Three pinch out abruptly to the southwest suggest a relatively small, steep-margined basin that included transitions from alluvial fan to fluvial to lacustrine depositional environments within a few square miles. The Horned Toad basin may have formed as a small sag basin along the active Garlock fault.

Brown siltstones and sands at the base of Member Four indicate a reversal in the fining upward trend seen in Members One through Three. Members Four and Five record renewed influx of arkosic and volcanic detritus and a basinward shift in facies. Lacustrine and lake margin environments were replaced by fluvial and alluvial fan deposits that ultimately filled the basin. The predominance of Bobtail Quartz Latite clasts in Member Five suggests that the dominant source area for the alluvial fans, during this final phase of basin filling, was to the south and southwest.

Structural History

The Horned Toad Formation has been deformed into a series of open folds cut by high angle faults (Figures 3 and 22). The dominant trend of these structures is southwest-northeast, subparallel to the Garlock fault. As noted above, the Cameron Granodiorite that forms the basement for the Horned Toad sediments is also apparently folded and cut by high angle faults. This structure is evident from the steep southeast dip of the basal contact of the Horned Toad Formation on the granitic basement and by faults exposed in the western Horned Toad Hills. In the northwest guarter of Section 34 (T12N. R13W. SBBM), a well-exposed fault dips approximately 80° to the southeast and exhibits reverse displacement with Cameron Granodiorite on the south juxtaposed against Member One sediments on the north (Figure 22, C-C'). Other faults exposed in Section 5 appear to have normal displacement juxtaposing basement against Member One strata. Along these faults, beds dip at high angles into the basement, and 1-2 m of fault rock (gouge and/or clay smear) is locally visible along the fault traces.

May (1981a) presented limited paleomagnetic data from the Cameron Granodiorite along the southeast side of Cameron Ridge that he inter-



FIGURE 22. 1:1 structural cross-sections through the Horned Toad Hills. Contractional deformation of the Horned Toad Formation and underlying granitic basement is related to southeast vergent reverse faults.

preted as consistent with approximately 50° - 60° of down-to-the-southeast rotation of the basement about a sub-horizontal axis trending sub-parallel to the trace of the Garlock fault. This hypothesis needs to be tested with a more complete sampling and spatial analysis of paleomagnetic data.

The name "Warren Syncline" has occasionally been used as a synonym for the Horned Toad Hills because of the major fold in the northeastern area of exposures (Figure 3). The axis of this syncline trends N50E and plunges gently to the northeast. The entire Horned Toad Formation is exposed on the north limb with bedding attitudes decreasing from 60° southeast near the basal contact. The south limb of the Warren syncline, which generally dips 10° – 20° to the northwest, is itself folded into an anticline and cut by a high-angle reverse fault (Figure 22, A-A'). The main fault in Section 36 (T12N, R13W, SBBM) is roughly axial planar to the anticline, and beds on the south limb exhibit moderately steep $(35^{\circ} - 60^{\circ})$ dips to the southeast and are unconformably overlain by Older Alluvium. Farther northeast along the south limb of the syncline, the reverse fault is apparently offset by an inferred northwest trending fault. Continuing northeast of this structure, the south limb is folded into a southeast vergent, asymmetric anticline with no associated reverse fault at the surface (Figure 3). The faulted south limb of the Warren syncline is interpreted as a fault propagation fold that likely involves basement. As described above, it is the faulted portion of this south-limb anticline that Dibblee (1967) interpreted as an angular unconformity.

In the central outcrop area (Section 35, T12N, R13W, SBBM), the dominant structure is a southeast dipping, asymmetric anticline (Figure 22, B-B'). This open fold has an axial surface that trends sub-parallel to the trend of the Warren syncline. This gentle anticlinal structure may be laterally equivalent to the fault propagation fold along the south limb of the Warren syncline. It is plausible that the antiform is cored at depth by a basement involved reverse fault. The lateral change from a gentle anticline to a tight, faulted anticline is likely accommodated by northwest trending high-angle faults and secondary folds mapped in the northwest quarter of Section 36 (T12N, R13W, SBBM) (Figure 3). The open anticline plunges gently to the southwest where it is cut by or merges with another high-angle reverse fault that juxtaposes Members Two and Four against Member One.

In summary, the dominant structural style of the Horned Toad Hills is one of southeast vergent, basement involved, fault propagation folds and reverse faults that are exposed at different structural elevations from southwest to northeast (Figure 22). These structures presumably root into the Garlock fault system and were active during the Pliocene to Pleistocene. Bartley et al. (1990) included the folds in the Horned Toad Formation on their map of Neogene contractional deformation within the Mojave block. Although all of the structures that they show adjacent to the San Andreas and Garlock faults are subparallel to those major structures (and therefore possibly kinematically linked), these authors argue for a regional pattern of north-south shortening that is consistent with slip on the major bounding structures and the northwest trending strike-slip faults within the western Mojave. Whether related to a regional contractional deformation or to local deformation along the Garlock fault, the structural history of the Horned Toad Formation reflects northwest-southeast oriented shortening during the Pliocene to Pleistocene.

Magnetic Polarity Stratigraphy

Paleomagnetic samples were collected from 12 sites in Members Two through Four of the Horned Toad Formation. Three to five separately oriented hand samples were collected at each of six sites in 1980 as described in May (1981a). At every site, samples were collected from the same bed and separated laterally by no more than 2 m.



FIGURE 23. 1. Vector demagnetization diagram for sample 4c during progressive alternating field demagnetization illustrates the removal of a secondary component interpreted to be a present field viscous remanance. 2. Vector demagnetization diagram for sample 5a during progressive alternating field demagnetization illustrates a very stable normal polarity component interpreted as detrital remanant magnetization.

The initial set of six sites was distributed stratigraphically through 18 m of section in the southeast quarter of Section 35 (T12N, R13W, SBBM). Oriented hand samples were cut to fit into plastic boxes and were measured on an SCT, three-axis, cryogenic magnetometer at the California Institute of Technology. Alternating field (AF) demagnetization was performed with a model GSD-5 Schonstedt specimen demagnetizer.

Stepwise alternating field demagnetization at 5 mT intervals up to 30 mT was performed on all specimens. Higher demagnetization steps up to 70 mT were performed on selected specimens. Natural remanent magnetization (NRM) intensities for 18 specimens ranged from 4.14 x 10-4 A/m to 1.27 x 10-1 A/m with a mean of 2.04 x 10-2 A/m. AF demagnetization up to 30 mT generally resulted in a loss of intensity from 30% to 95% of the NRM. Because of a viscous normal component present in most of the primary reversed samples, an initial increase in intensity was often observed.

The progressive demagnetization data from all specimens were analyzed with vector demagnetization diagrams (Figure 23). Final directions for each sample were calculated using a least squares regression to an operator designated portion of the demagnetization path. Analysis of the vector demagnetization diagrams indicated stable, primary paleomagnetic directions interpreted as a detrital remanent magnetization (DRM). Within each site, all three samples record the same polarity, but the dispersion was occasionally quite high. Within-site α_{95} values ranged from 8° – 102°. The magnetic polarity of each site was interpreted from analysis of the declination and inclination data from each site plotted in a stratigraphic framework. Sites one through four record a lower zone of reversed polarity extending through the lower 13 m of Member Two. Sites four and five exhibit normal polarity extending from the Lawlor Tuff into the base of Member Three at the sampled section.

A second suite of paleomagnetic samples was collected in 2006 to test and extend the original

TABLE 2. Paleomagnetic sites from which mean directions and latitudes of the site virtual geomagnetic pole could be calculated. Sites one and two yielded one sample each for which principle components analysis could be performed; MAD, maximum angular dispersion.

Locality	Ν	Dec	Inc	k (MAD)	a ₉₅	VGP Lat
Site 1	1	221.0°	-30.8°	-9.5		
Site 2	1	130.5°	-61.1°	-14		
Site 3	2	184.6°	-56.8°	68	44°	-85.6°
Site 4	5	225.4°	-49.2°	12	26°	-51.7°
Site 5	5	48.2°	51.7°	237	5.6°	50.2°

magnetostratigraphic interpretation. Five oriented samples were collected from each of six sites spanning approximately 14 m of section from the upper part of Member Two through the base of Member Four. Most samples consist of siltstone to fine-grained sandstone, and one site was collected from the Lawlor Tuff. Bedding orientations were taken at or near most sites for structural corrections. Samples were cut into 20 mm cubes, then incrementally demagnetized and measured on a 2-G Enterprises cryogenic magnetometer, located in a magnetically shielded room at the Berkeley Geochronology Center. After first measuring the NRM of all samples, they were subjected to alternating field demagnetization at 4, 6, 10, and 12 mT to erase any viscous remanant component. Stepwise thermal demagnetization followed in several steps from 90°C to 600°C using a modified ASC TD-48 thermal specimen demagnetizer.

Although magnetic polarity was determined for all sampled localities, only three of the six sites (three, four, and five) yielded data from which site mean directions could be calculated (Table 2). The processing was accomplished by averaging a sequential series of thermal demagnetization steps using principal components analysis (Kirschvink 1980), or by selecting a single temperature step considered representative of the mean direction of that sample. Analysis of samples collected at sites one, two, and six, failed to result in a stable linear vector decay toward the origin of the orthogonal vector diagrams on which the demagnetization data were plotted (Figure 24.1). However, polarity determinations for these sites were nonetheless unambiguous, based on the position and trend of the horizontal and vertical components as seen in equal area stereo plots of the data (Figure 24.2, 24.3).

The Lawlor Tuff (site five) was the only site sampled that yielded a "Class 1" normal polarity

(Figure 24.4), following Opdyke et al. (1977) and Johnson et al. (1982). The five samples analyzed yielded the following mean direction: Dec = 48.2° , Inc = 51.7° , k = 237, $\alpha_{95} = 5.6^{\circ}$ (Table 2). Samples from all other sites yielded reversed paleomagnetic signatures, with only sites three and four allowing calculation of mean directions; they are considered "Class 2" sites. One sample each from sites one and two (of five collected at each site) was suitable for principle components analysis. Results are listed in Table 2.

The new paleomagnetic data generally confirm the original magnetic polarity zonation of May (1981a), indicating that the Warren Local Fauna (stratigraphically below the Lawlor Tuff) is from sediments of reversed polarity. The normal polarity of the Lawlor Tuff is confirmed and two of the sites from our 2006 sampling (Site 3, Site 4) extend the original polarity stratigraphy of May (1981a) higher into Member Three and the base of Member Four. Both of these sites are interpreted as reversed polarity, constraining the normal polarity magnetozone to 3 to 10 m in stratigraphic thickness (Figure 62).

The following correlation of the Horned Toad Formation magnetostratigraphy is based on the time scale of Lourens et al. (2004). The basal reversed magnetozone representing most of Member Two is interpreted as Chron 3n.3r (4.896 -4.997 Ma) primarily based on the recognition of the 4.83 Ma Lawlor Tuff as the lowermost site in the overlying normal polarity zone. The normal polarity magnetozone that includes the Lawlor Tuff is interpreted as Chron 3n.3n (Sidufjall) (4.799 - 4.896 Ma), and the upper reversed polarity magnetozone is interpreted as Chron 3n.2r (4.631 - 4.799 Ma). This correlation relies heavily on the geochemical identification and Ar⁴⁰/Ar³⁹ age of the Lawlor Tuff and suggests that the age of Member Two of the Horned Toad Formation and the Warren Local



FIGURE 24. 1. Orthogonal vector diagram representative of sample demagnetization that did not allow calculation of a mean direction using principle components analysis (solid circles represent declination, or horizontal component; open squares represent inclination, or vertical, component); 2 and 3. Equal area stereo plots showing unambiguous polarity determinations based on the position and trend of the horizontal and vertical components for samples in which mean directions could not be calculated using principle components analysis (solid circles represent magnetic directions in the lower hemisphere; open squares represent magnetic directions in the upper hemisphere). 4. Orthogonal vector diagram representative of sample demagnetization from which a mean direction could be calculated using principle components and vertical or could be calculated using principle components and vertical or could be calculated using principle components and vertical or could be calculated using principle components and vertical or could be calculated using principle components and vertical or could be calculated using principle components and vertical or could be calculated using principle components analysis. 5. Equal area stereo plot showing mean directions of normal and reversed sites.

Fauna contained therein is approximately 4.85 – 5.0 Ma. Fossils from sites RV-8103, RV-8104, RV-8117, and possibly RV-8124 in Members Three and Four are 4.63 – 4.80 Ma (Figure 62). This correlation differs from that of May (1981a, b), and May and Repenning (1982), who interpreted this lower reversed polarity magnetozone as Chron 3An.1r (reversed interval in Chron 5 of earlier terminology).

The mean direction of the "Class 1" normal polarity site five, as seen in Figure 24.5, indicates that the Horned Toad Hills region has been rotated clockwise about a vertical axis by approximately 48°. Although the data for reversed polarity sites is highly scattered (k = 8.3, alpha₉₅ = 19°), the mean for these sites (Dec = 203.6°, Inc = -56.5°; Figure 24.5) also indicates clockwise rotation and is within 25° of being antipodal to the normal direction. Discordant paleomagnetic directions implying clockwise rotation of the western Mojave Desert were previously reported by Golombeck and Brown

(1988) who observed modest clockwise rotation (23.8 \pm 11.3°) in Miocene volcanic rocks southeast of the Horned Toad Hills.

MAMMALIAN PALEONTOLOGY

Warren Local Fauna

Since the early 1900s, a moderately large assemblage of fossil mammals has been collected from the Horned Toad Formation. C.L. Baker (U.C. Berkeley) first reported fossils from this area in 1911 (Reynolds et al. 1991). A. Alexander and L. Kellogg, also from U.C. Berkeley, collected additional specimens in 1925, and R. A. Stirton recovered more fossils in 1938 (Figure 25.1). The collections were significantly expanded by W. Daily, G. Gustely, and others from U.C. Riverside from the 1960s through the early 1980s (Figure 25.2). May (1981a) described the mammalian fossils from the Horned Toad Hills in a Master's thesis at U.C. Riverside under the direction of M.O.



FIGURE 25. 1. UCMP locality V-2503 in Member Two on the north limb of the Warren syncline. This quarry was developed by Annie Alexander and Louise Kellogg from UC Berkeley in 1925. 2. Locality RV-6834 (just right of back pack) where W.R. Daily and colleagues collected the skeleton of *Rhynchotherium* cf. *R. edensis*.

Woodburne. The U.C. Riverside specimens are now housed at the University of California Museum of Paleontology at U.C. Berkeley. When the collection was transferred to Berkeley, specimen numbers were modified by replacing the prefix of UCR with UCMP and adding the number 3 to the original numeric designation. Locality numbers were unchanged.

This collection of stratigraphically associated fossils is referred to as the Warren Local Fauna and includes 24 identified mammalian taxa:

shrew Cryptotis sp. mole cf. Scapanus rabbits Hypolagus vetus, Hypolagus edensis ground squirrel ?Spermophilus sp. gopher Prothomomys warrenensis n. gen., n. sp. pocket mouse

Perognathus sp.

mice

Repomys gustelyi, Postcopemys valensis, Peromyscus sp. A, Peromyscus sp. B, Jacobsomys dailyi, n. sp.,

dog

Borophagus cf. B. secundus

bear

cf. Agriotherium

saber-tooth cat Machairodus sp. cf. M. coloradensis

proboscideans

Rhynchotherium sp. cf. R. edensis, Pliomastodon vexillarius

horse

Dinohippus edensis

rhino

Teleoceras sp. cf. T. fossiger

peccary cf. *Prosthennops* sp.

camels

Megatylopus sp. cf. *M. matthewi*, *Hemiauchenia vera*, *Camelidae* gen. et. sp. indet.

antelope

cf. Sphenophalos

We have chosen to follow McKenna and Bell (1997) for classification of mammals at the ordinal level.

SYSTEMATIC PALEONTOLOGY

Order SORICOMORPHA Gregory, 1910 Family SORICIDAE Fischer de Waldheim, 1817 Subfamily SORICINAE Fischer de Waldheim, 1817 Tribe BLARININI Stirton, 1930

> Genus CRYPTOTIS Pomel, 1848 *Cryptotis sp.* Figures 26 – 33

Material: UCMP 317826 – left mandible with M_{1-3} , right maxillary with M^{1-2} , left maxillary with P^4 - M^2 ; UCMP 317891 – right M_2 ; UCMP 317892 – left mandible fragment with I_1 ; UCMP 317895 – right I_1 ; UCMP 317896 – right P^4 ; UCMP 317897 – upper incisor; UCMP 317898 – upper incisor.

Localities: All specimens were recovered from locality RV-7702.



FIGURE 26. Dental terminology used in the description of *Cryptotis n. sp.* Line drawings are of *Cryptotis* n.sp.

Diagnosis: A species of the genus *Cryptotis* in which the talonid of M_3 is crescent shaped. The talonid is less reduced than in *Cryptotis adamsi* (Hibbard) or *Cryptotis parva* (Hay), but lacks a distinct entoconid as observed in *C. gracilis*, *C. endersi*, and *C. magna*. The talonids of M_1 and M_2 are not shortened anteroposteriorly. The mental foramen is located midway between the protoconid and the hypoconid of M_1 . The coronoid process is not deflected labially or lingually, and there is no coronoid spicule. There is no post-mandibular canal. The interarticular area of the mandibular condyle is narrow (Figure 31). P³ is present but much reduced. P⁴, M¹, and M² possess deep posterior emaginations.

Description: The maxillaries and mandible that are assigned specimen number UCMP 317826 were found associated within a small block of



FIGURE 27. Mandibular terminology used in the description of *Cryptotis n. sp.* Line drawings are of *Cryptotis* n. sp.

matrix and show the same amount of wear. They are therefore considered to represent one individual and much of the following description is based on this specimen. Morphologic terminology utilized for the following description is illustrated in Figures 26 and 27.

M₁ of UCMP 317826 is well worn (Figure 28). In lingual view, the protoconid and metaconid are much taller than the paraconid (Figures 29, 30). The metaconid is placed transversely posterior to the protoconid, and the trigonid appears to be transversely compressed. The talonid is less compressed anteroposteriorly than in C. adamsi or C. parva and is slightly wider than the trigonid. The metalophid originates approximately two-thirds of the way up the side of the protolophid just labial to the midline and projects posteriorly to the hypoconid. The hypolophid projects lingually from the hypoconid to the posterior side of the entoconid. The entoconid is very worn, however, it is clear that there was no entoconid crest. The lingual cingulum is weakly developed, but the labial cingulum is



FIGURE 28. *Cryptotis* n. sp. (UCMP 317826): occlusal view of tooth row M₁ - M₃ from left to right. SEM image. Scale equals 1 mm.



FIGURE 29. *Cryptotis* n. sp. (UCMP 317826): lingual view of tooth row M₁ - M₃ from right to left. SEM image. Scale equals 1 mm.



FIGURE 30. *Cryptotis* n. sp. (UCMP 317826): labial view of tooth row and horizontal ramus with M_1 at left. Note position of mental foramen beneath M_1 . SEM image. Scale equals is 1 mm.



FIGURE 31. *Cryptotis* n. sp. (UCMP 317826): posterior view of articular condyle, ascending ramus, and dental foramen. SEM image. Scale equals is 1 mm.



FIGURE 32. *Cryptotis* n. sp. (UCMP 317826): lingual view of articular condyle with internal temporal fossa and dental foramen. SEM image. Scale equals is 1 mm.

strong from the anterior edge of the paraconid to the posterior edge of the hypoconid where it abuts the M_2 .

 M_2 is very similar to M_1 , but differs in the following characteristics: it is slightly smaller, and the trigonid does not appear to be as compressed transversely because the metaconid is placed relatively more anterior in relation to the protoconid. The anterolabial cingulum is stronger and extends further up the anterior edge of the paraconid. UCMP 317891 is less worn than UCMP 317826 and shows a prominent entoconid with no entoconid crest. The hypolophid extends to the posterolabial side of the entoconid, but does not connect to it at this early stage of wear.

 M_3 is much smaller than M_1 or M_2 . The protoconid and metaconid are transversely opposed, and the metaconid is relatively small. The talonid is strongly reduced, but is worn to a crescentic pattern suggesting that the reduction is not as advanced as in *C. adamsi* or *C. parva*. No distinct entoconid is present as in *C. gracilis*, *C. endersi*, and *C. magna*. The talonid is rotated slightly to the lingual side of the tooth.

All lower molars are pigmented at the tips of the cusps. The lower incisor is simple with one distinct node at the anterior tip and one weak node at the posterior end of the enamel. Both nodes are lost with wear. The alveoli preserved on UCMP 317892 indicate a double rooted antemolar (P_4 ?) and an incisor. The horizontal ramus is slender with the mental foramen located midway between the protoconid and hypoconid of M_1 . The dental foramen is located below and slightly towards the anterior edge of the internal temporal fossa. The internal temporal fossa is roughly triangular as in *C. adamsi* or *C. parva*.

The superior and inferior articular surfaces of the mandibular condyle are separated by a relatively long and narrow interarticular area with a lingual emargination (Figure 31). The inferior articular surface is placed anterior and slightly lingual to the superior surface and is posterior to the inferior sigmoid notch (Figure 32). The inferior articular surface is roughly rectangular in shape while the superior surface is more approximately triangular. The entire condyloid process is deflected lingually.

 P^3 is only represented by a broken base on UCMP 317826, but it would appear to be much reduced relative to P^4 .

P⁴ has a very strong posterior emargination and a strong posterior cingulum from the labial edge of the tooth to the vertex of the emargination.



FIGURE 33. *Cryptotis* n. sp. (UCMP 317826): occlusal view of upper tooth row with P⁴ - M² from left to right. SEM image. Scale equals is 1 mm.

The paracone and metacone are strongly connected and compressed transversely to form a labial shearing blade. A small parastyle is located near the anterior edge of the paracone. The protocone is small at the anteromedial edge of the tooth and is connected labially to the parastyle by a narrow crest. The hypocone is merely an inflation on the well developed hypoconal crest that connects anteriorly with the protocone at a moderate stage of wear. A very weak anterolabial cingulum is present.

M¹ is trapezoidal in shape with a strong posterior emargination (but weaker than in P⁴) (Figure 33). The parastyle is strong and essentially extends the posterior edge of the shearing blade of P⁴. The paracrista is short and perpendicular to the axis of the tooth row while the metacrista is long and sweeps posterolabially to the metastyle. The metacone is larger than the paracone. The mesostyle is placed just posterior to the labial junction of the paracone and the metacone. The protocone is well developed at the anterolingual edge of the tooth. As in P⁴, the hypocone is merely a slight anterior inflation on the hypoconal crest and is lingual to the posterior extension of the protocone. The hypoconal crest projects posteriorly and curves to the posterior edge of the tooth. A very weak cingulum is present anterior of the protocone while a slightly more prominent lingual cingulum extends from the base of the protocone to the base of the hypocone. A posterior cingulum is developed as in the P⁴.

 M^2 is smaller than the M^1 and is rectangular in shape with weaker cingula. No M^3 is known. The upper incisors are simple and uncleft. The facial fossa on the maxillary is deep and posteriorly pocketed extending from above the metacone of P^4 to above the mesostyle of M^1 . The pre-orbital bar is wide and extends back to above the mesostyle of M^2 .

Discussion: A number of criteria indicate that the shrew from the Warren Local Fauna is best assigned to the genus Cryptotis. The presence of an internal temporal fossa shows that it is a soricid rather than a Heterosoricine; the separation of the articular surfaces, the lingual emargination of the interarticular area, and the presence of pigmentation on the molars show that it belongs to the family Soricinae; the complete lack of an entoconid crest shows that it belongs to the tribe Blarinini and the reduced talonid of M₃, the posterior emargination of P⁴-M², the strong curving hypoconal crest of P⁴-M², the origination of the zygomatic process opposite the metacone or metastyle of M², and the relatively narrow interarticular area of the mandibular condyle indicate assignment of these specimens to Cryptotis.

Repenning (1967) assigned a fragmentary specimen from the Hemphillian, Christmas Valley Fauna of Oregon to *Cryptotis adamsi* as the oldest occurrence of this genus. Re-examination of that specimen indicates that it is not *Cryptotis* because of a well developed entoconid crest on M_1 . *Cryptotis sp.* from the Warren Local Fauna may be the

oldest known record of this genus although Wagner (1981) reported *Cryptotis* from the late Hemphillian Modesto Reservoir Local Fauna.

All species of Cryptotis, except the questionably assigned C. meadensis Hibbard (1953), lack an entoconid crest but retain a strong entoconid. This character is diagnostic of the tribe Blarinini that Repenning (1967) suggested was derived from a primitive "sorex" form such as Antesorex in the early Miocene. He proposed a phylogeny involving the Barstovian genus Adeloblarina giving rise to both the Blarina and Cryptotis lineages. Cryptotis sp. exhibits certain primitive characters that differentiate it from younger species. Some of these characters are also observed in Adeloblarina and include: lack of labial deflection of the coronoid process, the anterior position of the mental foramen, and the slenderness of the horizontal ramus and coronoid process. Unfortunately, no $\ensuremath{\mathsf{M}}_3$ is known from Adeloblarina to compare with the Cryptotis sp. in which this feature is less reduced (i.e., less derived) than in younger species.

The lack of a coronoid spicule and the minimal anteroposterior shortening of the talonid of M1-2 in Cryptotis sp. are two characters that appear to approach the primitive soricine condition closer than does Adeloblarina. For these reasons, Cryptotis sp. is probably not a direct descendent of Adeloblraina, however, these features do not exclude Cryptotis sp. from being ancestral to later species of Cryptotis. This evolutionary progression would require further reduction of the talonid of M₃, the anteroposterior shortening of the talonids of M₁₋₂, the posterior migration of the mental foramen, the labial deflection of the coronoid process, and the development of the coronoid spicule. All of these characters are realized in the early Blancan form Cryptotis adamsi.

No upper teeth are known from *Adeloblarina*. The upper dentition of *Cryptotis sp.* is relatively primitive with the retention of P^3 and the deep posterior emargination of P^4 -M². These features are similar to the primitive soricine condition as seen in *Antesorex*.

Cryptotis sp. is consistent with the suggestion by Repenning (1967) that the tribe Blarinini was derived from the primitive Soricini complex in the Miocene. The suite of characters in *Cryptotis sp.* contrasted with that of *Adeloblarina* suggests that more than one lineage attained the blarininine stage of evolution during the Miocene. *Cryptotis* from the Warren Local Fauna probably represents an undescribed species. Due to the limited amount



FIGURE 34. cf. Scapanus (UCMP 320597) humerus.

of material presently available, a new name is not proposed here.

Order ERINACEOMORPHA Gregory, 1910 Family TALPIDAE Fischer de Waldheim, 1817 Subfamily TALPINAE Fischer de Waldheim, 1817 cf. *Scapanus* Pomel, 1848

Material: UCMP 320133 – partial edentulous right mandible, UCMP 320134 – partial edentulous right mandible, UCMP 320135 – partial edentulous left mandible, UCMP 320597 – humerus.

Localities: Specimens UCMP 320133, 320134, and 320135 - RV-7702; UCMP 320597 - RV-6834.

Description and Discussion: Three mandible fragments are toothless and lack mandibular condyles. The horizontal ramus is relatively slender although only the alveoli for M_2 and/or M_3 are preserved. Mandibular depth beneath the anterior alveolus of M_3 for each specimen is: UCMP 320133 – 2.2 mm, UCMP 320134 – 2.2 mm, and UCMP 320135 – 2.4 mm.

A humerus (UCMP 320597) is nearly complete, but lacks the greater tuberosity (Figure 34). It is slightly smaller and more slender than the (?)Scapanus humerus from the Thousand Creek Fauna, Nevada, figured by Merriam (1911). J.H. Hutchinson (personal commun., 1980) kindly studied a cast of the specimen and considered it to likely represent either Domninoides or Scapanus with the pectoralis scars being most similar to Scapanus. The mandible fragments are also consistent with a provisional identification of Scapanus sp. Scapanus schultzi Tedford is well represented from the Clarendonian to early Hemphillian Dove Spring Fauna (Whistler and Burbank 1992) approximately 48 km east of the Horned Toad Hills. Material referred to cf. Scapanus sp. has also been



FIGURE 35. (UCMP 320128) *Hypolagus vetus,* P₃ occlusal pattern

reported from the Lava Mountains in the Mojave Desert by Reynolds et al. (1991). The mole *Scapanus* is known from Clarendonian to Recent faunas in North America (Whistler and Burbank 1992).

Order LAGOMORPHA Brandt, 1855 Family LEPORIDAE Fischer de Waldheim, 1817 Genus HYPOLAGUS Dice, 1917

Hypolagus vetus Kellogg, 1910 Figure 35

Material: UCMP 320128 – right mandible fragment with P_3 - M_2 , UCMP 320129 – partial skull with RP³- M^2 and LP⁴- M^1 , UCMP 320138 – P_3 , UCMP 320139 – miscellaneous molars, incisors, and post-cranial material.

Localities: UCMP 320128 - RV-6834, UCMP 320129 and UCMP 320139 - RV-7702, and UCMP 320138 - RV-8130.

Description and Discussion: The diagnostic characters used to assign this material to *Hypolagus vetus* Kellogg are the relatively large size of this rabbit and the morphology of P_3 . Both P_3s (UCMP 320128 & 320138) have relatively shallow anteroexternal reentrants and deep posteroexternal reentrants (Figure 35). The occlusal patterns compare well with *H. vetus* described by Dawson (1958) from the type locality at Thousand Creek, Nevada, and to the emended diagnosis for this taxon provided by White (1987). The anteroposterior length of UCMP 320128 is 3.3 mm, and the transverse diameter is 3.2 mm. The size of this specimen corresponds to the largest size observed

by Dawson (1958) for the topotypic material from Thousand Creek and is within the range of more than 90 samples measured by White (1987). The same dimensions for UCMP 320138 are 2.9 mm x 2.5 (+) mm at the occlusal surface, but this tooth is less worn than UCMP 320128, and the dimensions would increase significantly with wear.

The anteroexternal reentrant extends approximately 24% across the occlusal surface while the posteroexternal reentrant extends 52%. This compares well with values documented by White (1987) for *H. vetus*. The posteroexternal reentrant is deflected slightly to the anterior. The anterior wall of both P_3 s has a very faint dorso-ventral groove differing from the deeper anterior reentrant in both *H. oregonensis* Shotwell and *H. ringoldensis* Gustafson.

White (1987) considered *Hypolagus vetus* to be restricted to the Hemphillian and Blancan of the western USA and Baja, California.

Hypolagus edensis Frick Figure 36 Table 3

Material: UCMP 320603 - P₃, UCMP 320604 - P₃, UCMP 320605 - P₃, UCMP 320606 - P₃,



FIGURE 36. *Hypolagus edensis*, P₃ occlusal patterns, A (UCMP 320607), B (UCMP 320604), C (UCMP 320606), D (UCMP 320605), arrows point toward anterior.

TABLE 3. P_3 measurements for *Hypolagus edensis*. Dimensions in mm.

Specimen	A.P.	Т.
UCMP 320604	2.5	2.0
UCMP 320605	2.4	-
UCMP 320606	2.6	2.0 (+)
UCMP 320607	2.5	1.9

(A.P. = antero-posterior dimension, T. = transverse dimension)

UCMP 320607 – P₃, UCMP 320608 – P₃, UCMP 320601 – P², UCMP 320602 – P², UCMP 320596 – P², UCMP 320609 – associated right and left maxillaries with P³-M², UCMP 320610 miscellaneous molars.

Localities: UCMP 320609 – locality RV-6834. All other specimens were collected from locality RV-7702.

Description and Discussion: A second rabbit is present in the Warren Local Fauna and is readily distinguished from *Hypolagus vetus* by its much smaller size and by a deeper anteroexternal reentrant (Figure 36). White (1987) characterized *H. edensis* in his emended diagnosis as distinguishable from other species by the presence of a deep and smooth sided anteroexternal reentrant on P₃.

The posteroexternal reentrant of P₃ in the Warren specimens extends lingually 50% of the way across the occlusal surface (n=3) consistent with the 45-59% range reported by White (1987) for this taxon. The posterior wall of this reentrant possesses a distinct anterior inflation as figured in numerous specimens of H. edensis by White (1987). The anterolabial reentrant extends 32-33% across the occlusal surface comparing well with the 24-46% range reported by White (1987). The holotype of this taxon represents an extreme in the morphologic variability with the anteroexternal reentrant being subequal in occlusal extent to the posteroexternal reentrant. White (1987) also noted that the holotype is the smallest example of this species and is from an immature individual. Both antero- and posteroexternal reentrants of the P3 of H. edensis from Warren are filled with cement. The occlusal outline of P3 is variable although the lingual wall is generally rounded.

Hypolagus edensis is known from Hemphillian faunas of Arizona and California (Redington, Mt. Eden, Pinole) and the Blancan of California, Idaho, Nevada, Texas, and Washington (White 1987).

Order RODENTIA Bowdich, 1821 Family SCIURIDAE Fischer de Waldheim, 1817 Subfamily SCIURINAE Fischer de Waldheim, 1817 Genus SPERMOPHILUS Cuvier, 1825 ? Spermophilus sp. Figures 37, 38 Table 4

Material: UCMP 320106 – M₂, UCMP 320107 – P⁴, UCMP 320104 – M₁, UCMP 320108 – M¹ or ², UCMP 320105 – M₁, UCMP 320099 – M₂.

Locality: All specimens were collected from locality RV-7702.

Description and Discussion: Six isolated teeth questionably are assigned to the genus *Spermophilus* Cuvier. A P⁴ (Figure 37) is triangular with a strong parastyle connected labially to the paracone. A strong protoloph connects the paracone and the protocone while a weaker metaloph connects the protocone to the metacone.

A worn upper molar $(M^{1} \text{ or } ^{2})$ is approximately square with a strong protocone that joins both anterior and posterior cingula. The protoloph projects to the anterolabial edge of the protocone, but the metaloph terminates labially of the protocone.



FIGURE 37. *?Spermophilus* sp. (UCMP 320107), occlusal view of P⁴. SEM image. Scale equals 1 mm.



FIGURE 38. *?Spermophilus* sp. (UCMP 320104), occlusal view of M₁. SEM image. Scale equals 1 mm.

The lower dentition is represented by two M₁s and two M₂s. The M₁s are subquadrate with partially closed trigonid basins (Figure 38). The mesostylid is very weak or absent with a relatively wide valley between the metaconid and the entoconid. This condition differs from species of *Spermophilus* such as *S. shotwelli* Black or *S. argonautus* Stirton and Goeriz (1942) that are anteroposteriorly compressed. The relative lack of anteroposterior compression resembles Black's (1963) description of *S. wilsoni* Shotwell. The entoconid is strongly connected to the posterolophid.

The squirrel from the Warren Local Fauna tentatively is assigned to the genus *Spermophilus*. However, its specific identity is not clear. It is approximately the same size as *S. gidleyi* or *S. argonautus* and is smaller than *S. wilsoni* and *S. shotwelli*. It differs from both *S. gidleyi* and *S. argo*-

TABLE 4. Measurements of *?Spermophilus* sp. Dimensions in mm.

Specimen	A.P.	т.
UCMP 320107 P ⁴	1.78	1.87
UCMP 320108 M ^{1 or 2}	1.92	2.18
UCMP 320104 M ₁	1.95	2.07
UCMP 320105 M ₁	1.97	2.26
UCMP 320106 M ₂	2.09	2.38
UCMP 320099 M ₂	2.26	2.45



FIGURE 39. Prothomomys warrenensis n. gen. n. sp. occlusal view of paratype dP_4 (UCMP 320185). Scale equals 0.1 mm.

nautus in having lower molars less anteroposteriorly compressed. This, as well as the incomplete metaloph, closed trigonid basin on M_1 , and open (?) trigonid on M_2 , most nearly resemble characters of *Spermophilus wilsoni*.

Family GEOMYIDAE Bonaparte, 1845 Subfamily GEOMYINAE Bonaparte, 1845

> Prothomomys new genus Figures 39, 40

Diagnosis of Genus: A genus of the subfamily Geomyinae with very hypsodont, unrooted, cheek teeth; complete anterior enamel plates on upper and lower molars; DP₄ very similar to that of *Parapliosaccomys oregonensis* Shotwell.

Type Species: *Prothomomys warrenensis* new species.



FIGURE 40. *Prothomomys warrenensis* n. gen. n. sp. A: occlusal view of holotype P₄ (UCMP 320186), B: lateral view of same P₄ (UCMP 320186), C: Lateral view of paratype M¹ (UCMP 320188), D: occlusal view of same M¹ (UCMP 320188). SEM image. Scale equals 0.1 mm.

Etymology: Prefix *Pro* from Latin meaning before and *thomomys* from the existing name *Thomomys* Wied-Neuwied, 1837.

Prothomomys warrenensis n. sp. Table 5

Diagnosis of Species: Same as for genus.

Type series: UCMP 320186 – P_4 is designated as the holotype. UCMP 320815 – DP_4 and UCMP 320188 – M^1 are designated as paratypes.

Type locality: The holotype and both paratypes were collected from locality RV-7702.

Specimens: UCMP 320187 – P_4 , UCMP 320189 – M^{1} or ², UCMP 320560 – M_3 , UCMP 320561 – M_3 , UCMP 320564 – $M_{1 \text{ or } 2}$, UCMP 320565 – $M_{1 \text{ or } 2}$, UCMP 320566 – $M_{1 \text{ or } 2}$, UCMP 320567 – M^{1} or ², UCMP 320568 – M_3 , UCMP 320569 – M^{1} or ², UCMP 320136 – M_1 or ² unworn, UCMP 320137 – M^{1} or ² unworn, UCMP – 124821 – M^{1} or ², UCMP 123629 – M^{1} or ², UCMP 320595 – M^{1} or ².

Localities: UCMP 320187 and UCMP 320595 - locality RV-6834, UCMP 123629 - locality V-6638, UCMP 124821 - locality V-2503. All other specimens are from locality RV-7702.

TABLE 5. Measurements of *Prothomomys warrenensis*.Dimensions in mm.

Specimen	A.P.	Т.
UCMP 320187 – P ₄	1.81	1.89 posterior
		0.78 anterior
UCMP 320185 – DP ₄	2.12	1.00
UCMP 320186 – P ₄	1.49	1.11 posterior
		0.85 anterior
UCMP 320188 – M ¹	0.99	1.65
UCMP 320569 - M ^{1 or 2}	0.92	1.50
UCMP 320189 - M ^{1 or 2}	0.84	1.06
UCMP 320595 - M ^{1 or 2}	0.95	1.42
UCMP 320567 - M ^{1 or 2}	1.07	1.65
UCMP 320566 - M _{1 or 2}	1.00	0.84+
UCMP 320564 - M _{1 or 2}	0.91	1.37
UCMP 320560 – M ₃	0.86	1.12
UCMP 320561 – M ₃	0.90	1.26
UCMP 320562 – M ₃	0.86	1.32

Etymology: The species name is derived from *warren* indicating the Warren Local Fauna or Warren syncline and from *–ensis* denoting place.

Description: Two permanent P_4 s are very hypsodont and rootless with well developed narrow dentine tracts. Both teeth are moderately worn with three of the four dentine tracts having breached the occlusal surface; the slightly shorter dentine tract is on the anterior lophid.

The occlusal pattern of the P_4 consists of a rounded anterior column narrowly connected to the antero-posteriorly compressed posterior column (Figure 39a and b). The anterior column will remain rounded throughout wear rather than becoming diamondshaped.

The dP_4 (UCMP 320185, Figure 40) is double rooted, low crowned, lophate, and has an occlusal pattern very similar to that of *Parapliosaccomys oregonensis* (Shotwell 1967).

The molars of the Warren gopher are very hypsodont with well developed, narrow dentine tracts (Figure 39c and d). The molars are generally rootless although UCMP 320568 (M_3) does have poorly developed roots and relatively shorter dentine tracts. The molars have enamel on both the anterior and posterior surfaces, and the anterior enamel plate is unreduced and continuous to the base of the tooth as in *Thomomys*. The occlusal shape of the molars is somewhat variable, but generally ellipsoid. UCMP 320564 (M_1 or 2) has a marked lingual constriction.

Discussion: The advanced degree of hypsodonty (primarily rootless) with presence of well developed narrow dentine tracts and continuous anterior enamel plates in both upper and lower molars suggest that Prothomomys n. gen. is closely related to, and probably ancestral to, the extant genus Thomomys Maximilian. Modern species of Thomomys are distinguished from other Geomyidae by having the lower molars with lingual constriction of lophids and upper molars with labial constriction of lophs. However, Zakrzewski (1969) noted that the majority of molars in Thomomys gidleyi, from the Blancan Hagerman Local Fauna, were not constricted, and Gustafson (1978) reported occlusal shape variable in molars of Thomomys sp. cf. T. gidleyi from the early Blancan White Bluffs Local Fauna.

Prothomomys n. gen. differs from *Parapliosaccomys oregonensis* (Shotwell, 1967) whose dentinal tracts are irregular, the anterior enamel plate is reduced in upper and lower molars, and the anterior column of P_4 becomes diamond-shaped with wear, rather than well rounded. Martin (1979) noted that "tear-shaped" molars are also developed in *P. oregonensis* from northern Oregon.

The Warren gopher is very advanced with respect to the degree of hypsodonty and development of dentine tracts, and the dP₄ suggests a close relationship with Parapliosaccomys oregonensis from the late Hemphillian of Oregon (Shotwell 1967). Prothomomys n. gen. retains an isolated posterior lophid on DP₄ that later becomes anteriorly connected in Thomomys. Various authors including Shotwell (1967), Zakrzewski (1969), and Martin (1979) have proposed that P. oregonensis was ancestral to Thomomys. If this were true, then the Warren gopher might represent an intermediate form between these two taxa. However, reduction of the anterior enamel plates on the lower molars of P. oregonensis makes it unlikely that P. oregonensis was ancestral to Thomomys. It is also unlikely that Prothomomys was derived from P. oregonensis because Prothomomys has continuous anterior enamel plates as in Thomomys. The Warren gopher therefore provides a potentially better ancestor for Thomomys than does P. oregonensis. The very close similarity in dP4s suggests that Prothomomys n. gen. was probably derived from Pliosaccomys as was Parapliosaccomys.

These observations suggest a phylogeny in which both Prothomomys and Parapliosaccomys were derived from Pliosaccomys during the Hemphillian. Martin (1979) has convincingly demonstrated the evolution of Pliosaccomys through Parapliosaccomys in Oregon during the Hemphillian. This evolution was characterized by an increase in hypsodonty and the development of dentine tracts. In Parapliosaccomys oregonensis, however, the anterior enamel plates of the lower molars are strongly reduced. Prothomomys warrenensis also developed hypsodont cheek teeth with well defined dentine tracts and no roots. More importantly, P. warrenensis does not show reduction of the anterior enamel plates on the lower molars. Prothomomys may have been ancestral to Thomomys cf. T. gidleyi by the early Blancan (Ringold Formation, Gustafson, 1978).

There are two described fossil species of *Thomomys* in North America: *T. gidleyi* Wilson (1933) (Hagerman, Idaho; San Timoteo Badlands, California; Ringold, Washington) and *T. carsonensis* Kelly (1994) (Fish Spring Flat Local Fauna, Nevada). All of these occurrences are in Blancan faunas. Unnamed species of *Thomomys* are reported from the Blancan faunas of the San Timoteo Badlands (Albright 1999), the Blancan Grand View Fauna, Idaho (Hearst 1998), the Blancan – Irvingtonian Anza-Borrego faunas of California



FIGURE 41. 1. *Perognathus* sp., (UCMP 320182) occlusal view of P_4 . SEM image. Scale equals 0.1 mm. 2. *Perogna-thus* sp., (UCMP 320182) oblique view of P_4 . SEM image. Scale equals 0.1 mm.

(Becker and White 1981), the Late Hemphillian Santee and Devil's Nest Airport Local Faunas of Nebraska (Voorhies 1990), and the Clarendonian Iron Canyon and Dove Spring Faunas in California (Whistler and Burbank 1992). Tedford et al. (2004) list *Thomomys* (*Plesiothomomys*) as a taxon within the characterizing fauna of the late late Hemphillian (Hh4; Tedford et al. 2004). However, all described species of *Plesiothomomys* are from Pleistocene faunas. Suggested occurrences of *Thomomys* in the late Hemphillian and even Clarendonian may indicate a more complex phylogeny for *Prothomomys*, *Thomomys*, *Pliosaccomys*, and *Parapliosaccomys*, or an incomplete record of the ranges of these taxa.

Family GEOMYDIAE Bonaparte, 1845 Subfamily HETEROMYINAE Gray, 1868 Genus PEROGNATHUS Wied-Neuwied, 1839

> ? Perognathus sp. Figure 41

Material: UCMP 320182 – P₄, UCMP 320183 – M₁ or 2, UCMP 320184 – M¹?

Locality: All specimens were collected from locality RV-7702.

Description and Discussion: Three isolated teeth from the Warren Local Fauna are questionably assigned to the genus *Perognathus* Wied-Neuwied. The dimensions of the P_4 (UCMP 320182) are square (0.83 mm x 0.83 mm) with the protolophid slightly narrower than the metalophid (terminology after Lindsay 1972). These lophids would

unite medially with moderate wear. In early wear, the protolophid is v-shaped, however, the anteromedial groove shallows quickly. Both labial and lingual reentrants are well developed with the labial one slightly shallower. Other than size, the morphologies of UCMP 320184 (M¹? 0.94 mm x 1.16 mm) and UCMP 320183 (M_{1 or 2}: 0.94 mm x 1.01 mm) are of little value for identification.

The P₄ (UCMP 320182, Figure 41) is comparable in size and morphology to *Perognathus gidleyi* Hibbard from the early Blancan Rexroad Fauna, Kansas. It differs from the holotype of *P. gidleyi* in that the Warren specimen has no posteromedial groove, and the labial reentrant is slightly shallower than the lingual. UCMP 320182 differs from *P. dunklei* Hibbard by its larger size, from *P. henryredfieldi* Jacobs by its larger size and medial junction of the lophids, from *P. mclaughlini* Hibbard by its smaller size and medial junction of the lophids.

Family MURIDAE Illiger, 1811 Subfamily SIGMODONTINAE Wagner, 1843 Genus REPOMYS May, 1981 *Repomys gustelyi* May, 1981

Repomys gustleyi is the most common rodent in the Warren Local Fauna (May 1981b). *Repomys* is a hypsodont cricetine that was originally described from three faunas in California and Nevada, and a complete description of *Repomys* from the Warren Local Fauna can be found in May (1981b). The etymology of this genus honors the late C.A. Repenning – i.e., Rep's mouse. The entire type series for *Repomys gustleyi* was collected from locality RV-7702 in Member Two of the Horned Toad Formation.

May (1981b) identified two additional species of Repomys, R. panacaensis from the early Blancan Panaca Local Fauna in Nevada and R. maxumi from the early Blancan Maxum Local Fauna in California. Repomys has since been recognized at a number of additional localities in the southwestern USA including R. gustelvi from Devil's Nest Airstrip and Santee faunas in Nebraska (Voorhies 1990), R. gustleyi from the Mt. Eden Local Fauna (Albright 1999), R. maxumi from the San Timoteo Badlands (May and Repenning 1982; Albright 1999), R. panacaensis from the Buckhorn Local Fauna in New Mexico (Morgan and Lucas 2003), Repomys n. sp. from the Panaca Local Fauna (Lindsay et al. 2002), and R. arizonensis from Arizona (Tomida 1987). All known species of Repomys, except for R. gustleyi, are from Blancan age faunas. Most authors have followed May (1981b) in considering Repomys to have a North American origin (e.g., Jacobs and Lindsay 1984), although Voorhies (1990) lists Repomys as a latest Hemphillian immigrant with no supporting discussion. Tedford et al. (2004) listed Repomys (R. gustelyi) as one of the defining taxa for the late late Hemphillian (Hh4) based on the known occurrences in the Warren, Mt. Eden, Santee and Devil's Nest Airstrip Local Faunas.

Genus POSTCOPEMYS Lindsay and Czaplewski (2011)

Korth (1998) described the genus Antecalomys as a sigmodontine cricetid, interpreted phyletically between the genus Abelmoschomys from Clarendonian deposits in Florida described by Baskin (1986) and the extant cricetid genus Calomys (interpreted by Baskin to include the extinct taxon Bensonomys as a subgenus) recorded from numerous Blancan faunas in North America, and possibly part of the sigmodontine cricetid radiation that occurred in South America during the late Pliocene (but see Pardiñas et al. 2002). Part of the rationale for the genus Antecalomys is development of an oblique ridge in lower cheek teeth formed by alignment of the entolophulid with the posterior arm of the protocone (which are not aligned in Copemys), and retaining nonalignment of paraconule II with the anterior arm of the hypocone in upper cheek teeth, resulting in the absence of an oblique ridge in those teeth. Korth (1998) also noted a weakly divided anteroconid and presence of an accessory rootlet in M1 on the genotype of Antecalomys, A. phthanus. Accessory rootlets on

upper and lower cheek teeth are characteristic of sigmodontine rodents. many Korth (1998) assigned two other known species, Copemys valensis (Shotwell 1967) and ?Copemys vasquezi (Jacobs 1977), to the genus Antecalomys, based primarily on development of an oblique ridge in lower teeth formed by alignment of the entolophulid with the posterior arm of the protocone and with nonalignment of paralophule II and the anterior arm of the hypocone in upper teeth. Lindsay and Czaplewski (2011) removed C. valensis and ?C vasquezi from the genus Antecalomys, considering that these taxa lack the development of accessory rootlets that are seen in some Sigmodontinae. They created the genus Postcopemys for the new species Postcopemys repenningi, from the early Blancan (and possibly late Hemphillian) Verde Formation in Arizona, and placed both C. valensis and ?C. vasquezi in the genus Postcopemys. Both Antecalomys and Postcopemys develop an oblique ridge in lower cheek teeth by alignment of the entolophulid and the posterior arm of the protocone, and lack an oblique ridge in upper cheek teeth (as in the genus Copemys) because protolophule II and the anterior arm of the hypocone are not aligned.

> Postcopemys valensis Shotwell (1967) Figure 42 Table 6

Material: UCMP 320575 – M₁, UCMP 320576 – M₁, UCMP 320577 – M¹

Locality: All specimens are from locality RV-7702.

Description and Discussion: A small species of Postcopemys is represented by three brachydont cheek teeth (two M₁s and one M¹). UCMP 320576 and UCMP 320577 are both abraded anteriorly, but size and other dental features compare favorably to casts of Postcopemys valensis from Hemphillian deposits in Oregon. UCMP 320575 is unworn and of similar size. On the unworn specimen the anteroconid is very broad, gently rounded anteriorly (lacking a groove) and steep posteriorly where an anterolophid is directed posteriorly to join the metalophid on the midline. The metaconid is placed close to the lingual side of the anteroconid, partly closing the anterolingual sinus after moderate wear. Anterior arms of the protoconid and hypoconid are short, joining the metalophid I and the entolophid I, respectively. Posterior arms of the protoconid and hypoconid are long, with the protoconid arm joining the entolophid and the hypoconid arm expanding to become the prominent posterior



FIGURE 42. Postcopemys valensis, (UCMP 320575), occlusal view of M1. SEM image. Scale equals 0.1 mm.

TABLE 6. Measurements of *Postcopemys valensis*. Dimensions in mm.

Specimen	A.P.	Т.
UCMP 320575 M ₁	1.32	0.78
UCMP 320576 M ₁	1.31+	0.81
UCMP 320577 M ¹	1.47	0.87

cingulum that is flexed anteriorly to join the posterior base of the entoconid. The posterior arm of the protoconid and the entolophid are slightly offset, but with slight wear they become aligned, which is characteristic for both *Antecalomys* (Korth 1998) and *Postcopemys* (Lindsay and Czaplewski, 2011). A mesolophid and other accessory cusps and lophs are absent. Roots are not preserved on the M1.

Genus PEROMYSCUS Gloger, 1841 *Peromyscus* sp. A Figure 43 Table 7

Material: UCMP 32570 – right mandible with M_{1-2} , UCMP 320571 – right mandible with M_2 , UCMP 320573 – M¹, UCMP 320574 – partial M¹, UCMP 123630 – partial M¹.

Locality: UCMP 126360 is from locality V-6638. All other specimens are from locality RV-7702.

Description: A medium size, brachydont mouse with oblique cusp alignment in upper and lower

molars is recorded from two mandibles, an isolated M¹, and two M¹ fragments. The occlusal outline of M¹ is elongate oval, longer than wide, with four main cusps (protocone, paracone, hypocone, and metacone) and a large subequally bilobed anterocone. Labial cusps are placed opposite to the posterior side of lingual cusps. The anterior arm of the protocone is long, joining the posterior base of the anterocone centrally. The posterior arm of the protocone is short, joining the anterior side of protolophule II near the midline. The anterior arm of hypocone is long, joining the posterior side of protolophule II, with alignment of these lophs. The posterior arm of the hypoconid is long, directed labially, and joins the metalophule II to become a short posterior cingulum that terminates at the posterior side of the metacone. The protolophule II and metalophule II are short, as is a mesoloph that extends labially from the anterior arm of the hypocone, posterior to its union with protolophule II. A short lingual cingulum descends from the lingual lobe of the anterocone, terminating as a low cingulum that partly closes the anterolingual sinus. Three prominent roots, one lingual and two labial, are developed; accessory rootlets are unknown.

The dentary includes a mental foramen that is relatively low and anterior, below the lowest position of the diastema, near the posterior ascension of the diastema. The masseteric crest terminates anteriorly below the anterior root of M_1 , well above the level of the mental foramen on UCMP 320570



FIGURE 43. 1. *Peromyscus* sp. A (UCMP 320570), occlusal view of M₁-M₂ in right dentary fragment. SEM image. Scale equals 1 mm. 2. *Peromyscus* sp. A (UCMP 320570), occlusal view of M₁-M₂. SEM image. Scale equals 2 mm. 3. *Peromyscus* sp. A (UCMP 320570), labial view of right dentary. SEM image. Scale equals 2 mm. 4. *Peromyscus* sp. A (UCMP 320574), occlusal view of M¹. SEM image. Scale equals 2 mm. 5. *Peromyscus* sp. B (UCMP 320572), occlusal view of M¹. SEM image. Scale equals 2 mm. 5. *Peromyscus* sp. B (UCMP 320572), occlusal view of M¹. SEM image. Scale equals 2 mm.

TABLE 7. Measurements of *Peromyscus* sp. A. Dimensions in mm.

Specimen	A.P.	Т.
UCMP 20570 M ₁	1.71	1.08
UCMP 20570 M ₂	1.40	1.10
UCMP 20571 M ₂	1.47	1.11
UCMP 20573 M ¹	1.78	1.18

and slightly above the level of the mental foramen on UCMP 320571.

The occlusal outline of M₁ is elongate triangular with a round anterior margin (Figure 43). Four main cusps (protoconid, metaconid, hypoconid, and entoconid) and a smaller, asymmetrical, single-cusped anteroconid are present. Lingual cusps are placed opposite to the anterior arms of labial cusps. The anterior arm of the protoconid is short, joining the posterior side of metalophid I that is directed anteriorly to join the posterior side of the anteroconid at the midline. The metaconid is placed relatively close to the anteroconid, and a narrow v-shaped valley separates these cusps. A long posterior arm of the protoconid joins the anterior side of entolophid I, and these lophs are aligned. A long anterior arm of the hypoconid joins the posterior side of entolophid I, while a long posterior arm of the hypoconid is flexed lingually to become a robust posterior cingulum that terminates short of the lingual tooth margin. There is no mesolophid, or other accessory styles or lophids. A labial anterior cingulum descends from the anteroconid, partly closing the anterolabial sinus; the labial sinus is partly closed by a low labial cingulum; lingual cingula are absent. Two well developed roots (anterior and posterior) are developed; accessory rootlets are unknown.

The occlusal outline of M2 is a rounded rectangle, longer than wide, with four main cusps, as in M₁ (Figure 43). Lingual cusps are placed opposite to the anterior arms of labial cusps, as in M₁. The anterior arm of the protoconid is short, joining the posterior side of metalophid I that continues anteriorly to join the high anterior cingulum at the midline. The posterior arm of the protoconid is long; it joins the anterior side of entolophid I slightly lingual to the midline, and these lophids are aligned, as in M₁. The anterior arm of the hypoconid is long; it joins the posterior side of entolophid I at the midline. The posterior arm of the hypoconid is long and flexed lingually to become a robust posterior cingulum that terminates short of the lingual tooth margin. There is no mesolophid or other accessory styles or lophids. The anterior labial cingulum descends gradually from the midline and is flexed posteriorly to terminate at the anterior base of the protoconid; there is no lingual anterior cingulum. The broad labial sinus is partly closed by a low

labial cingulum; lingual cingula are absent. Two roots are developed as in M_1 ; accessory rootlets are unknown.

Peromyscus sp. A is most similar to *P. kansasensis* from the Rexroad Fauna in Kansas (Hibbard 1941). It differs from *P. kansasensis* by its slightly smaller size, however, a larger sample size may reveal overlapping size ranges. *Peromyscus* sp. A is larger that *P. nosher* from the White Bluffs Local Fauna, Washington; *P. baumgarneri* from the Fox Canyon and Rexroad Faunas, Kansas; *P. cragini* from the Cudahy Fauna, Kansas; and *P. Hagermanensis* from the Hagerman Local Fauna, Idaho; Deer Park Fauna, Kansas; and the 111 Ranch Fauna, Arizona. *Peromyscus.* sp A is smaller than *P. antiquus* from the Thousand Creek Fauna, Nevada, and *P. pliocenicus* from the Kern River Fauna, California.

Miocene cricetid rodents in North America, commonly assigned to the genus Copemys, are characterized by non-alignment of oblique ridges on upper and lower cheek teeth. During the Pliocene cheek teeth of descendants of these Miocene cricetids gradually became aligned, primarily between the anterior arm of the hypocone and the paralophule II in upper teeth, and between the posterior arm of the protoconid and the entolophid I in lower teeth. The genus Antecalomys and the genus Postcopemys were both defined, in part, based on non-alignment of obligue lophs in upper teeth with alignment of oblique lophs in lower teeth. Most of the Pleistocene and extant species of Peromyscus can be characterized as having alignment of obligue lophs in both upper and lower teeth. In Antecalomys the upper teeth develop accessory rootlets, which are characteristic of some sigmodontine cricetids, and in Postcopemys none of the species develop accessory rootlets; Postcopemys is considered a probable member of the neotomine-peromyscine cricetid radiation, which also includes Copemys and the fossil and extant species of Peromyscus. The Warren Local Fauna is one of the few fossil records having species of both Postcopemys and Peromyscus as well as the hypsodont cricetid Repomys. Peromyscus sp. A may represent a new species of Peromyscus, however, due to the small sample size from the Warren Local Fauna, and the close comparison to P. kansasensis, we hesitate to name a new taxon for this material.

> Peromyscus sp. B Figure 43.5

Material: UCMP 320572 - M1.

Locality: UCMP 320572 is from RV-7702.

Description and Discussion: A second species of *Peromyscus* is represented by an isolated M¹ with clearly aligned anterior arm of the hypocone and paralophule II, as well as a bilobed anterocone. It is smaller than *Peromyscus* sp. A and the lobes of the anterocone are located closer together and separated by a shallower groove. The measurements of UCMP 320572 are: A.P. 1.71; T. 1.11.

Genus JACOBSOMYS Czaplewski, 1987 Jacobsomys dailyi new species

> Figures 44 – 46 Table 8

Holotype: UCMP 320583 – M^1 , UCMP 320578 – right mandible fragment with M_1

Paratype Material: UCMP 320579 – M_3 , UCMP 320580 – right maxillary fragment with M¹, UCMP 320581 – left mandible fragment with M₁, UCMP





FIGURE 44. 1. Jacobsomys dailyi n. sp. holotype specimen (UCMP 320578), labial view of right mandible with M_1 and dorsal position of dental foramen. SEM image. Scale equals 1 mm. 2. Jacobsomys dailyi n. sp. holotype specimen (UCMP 320578), occlusal view of right mandible with M_1 . SEM image. Scale equals 0.1 mm.



FIGURE 45. Jacobsomys dailyi n. sp. holotype specimen (UCMP 320583), occlusal view of M¹. SEM image. Scale equals 0.1 mm.



FIGURE 46. 1. Jacobsomys dailyi n. sp. (UCMP 320584), occlusal view of M¹. SEM image. Scale equals 2 mm. 2. Jacobsomys dailyi n. sp. (UCMP 320585), occlusal view of M². SEM image. Scale equals 2 mm. 3. Jacobsomys dailyi n. sp. (UCMP 320578), occlusal view of M₁. SEM image. Scale equals 2 mm. 4. Jacobsomys dailyi n. sp. (UCMP 320583), occlusal view of M₁. SEM image. Scale equals 2 mm. 5. Jacobsomys dailyi n. sp. (UCMP 320588), occlusal view of M₂. SEM image. Scale equals 2 mm. 5. Jacobsomys dailyi n. sp. (UCMP 320588), occlusal view of M₂. SEM image. Scale equals 2 mm. 6. Jacobsomys dailyi n. sp. (UCMP 320589), occlusal view of M₃. SEM image. Scale equals 2 mm.

Specin	nen	N	0.R.	x	S.D.
M ¹	L	3	1.70	1.70	0.0
	W	3	1.18-1.23	1.20	0.03
M ²	L	2	1.33-1.35	1.34	0.015
	W	2	1.08-1.23	1.16	0.11
M ₁	L	3	1.69-1.82	1.74	0.07
	W	3	1.06-1.08	1.07	0.01
M ₂	L	3	1.36-1.40	1.38	0.02
	W	3	1.11-1.18	1.15	0.04
M_3	L	2	1.25-1.33	1.29	0.06
	W	2	0.98-1.03	1.01	0.035

(N = number of specimens, O.R. = observed range, X = mean, S.D. = standard deviation.)

 $\begin{array}{l} 320582 - M_1, \mbox{ UCMP } 320584 - M^1, \mbox{ UCMP } 320585 \\ - M^2, \mbox{ UCMP } 320586 - M_2, \mbox{ UCMP } 320587 - M_2, \\ \mbox{ UCMP } 320588 - M_2, \mbox{ UCMP } 320589 - M_3, \mbox{ UCMP } \\ 320590 - \mbox{ partial } M_1, \mbox{ UCMP } 320591 - \mbox{ partial } M^1, \\ \mbox{ UCMP } 320592 - \mbox{ partial } M_2, \mbox{ UCMP } 320593 - M^2. \end{array}$

Referred Material: UCMP 320594 - M1.

Type Locality: RV-7702. All specimens were collected from RV-7702 except for UCMP 320594 that was collected from RV-8103.

Etymology: Named in honor of William R. Daily who collected and prepared most of the fossils in the original U.C. Riverside collection of the Warren Local Fauna.

Diagnosis: This small sigmodontine is represented largely by isolated brachydont cheek teeth with slight alternation of cusps in M1, the lingual being anterior to the labial. The major cusps of M¹ are nearly aligned. Both upper and lower first molars have strongly bilobed and symmetrical anterocones (ids). The M¹ of J. dailyi possesses a long, thin anteroloph between the labial anterocone and the paracone, a long, thin mesoloph confluent with the posterior base of the paracone and adjacent to the base of the paracone on M². M₁ includes a long thin mesolophid that is confluent with the anterior base of the entoconid. The anterior mure and the median mure are both anteroposteriorly oriented although deflected slightly labially anterior to posterior. Jacobsomys dailyi differs from J. verdensis by its smaller size, slightly lower length-width ratio on M¹, and symmetrical anteroconid on M_1 .

Description and Discussion: The double rooted M_1 has a relatively wide and strongly bilobed anteroconid. A labial cingular shelf is well developed as is the posterior cingulum that projects from the hypoconid to the posterior base of the entoconid. UCMP 320578 (Figure 44) is only slightly worn and shows a slight non-alignment of the entolophid and the posterior arm of the protoconid. A well developed mesolophid connects with the anterior side of the entoconid forming a shallow enamel lake that is lost with wear.

 M_2 has a moderately well developed anterior cingulum and a strong posterior cingulum with a small mesostylid (Figure 46.5). A prominent mesol-ophid is present, and this tooth has two roots.

The M¹ has a strongly bilobed anterocone plus a long thin anteroloph and a mesoloph (Figures 45 and 46). The primary cusps (protocone – paracone and hypocone-metacone) are arranged nearly opposite one another. The anterior mure joins the anterocone at the midline of the tooth. The mesoloph connects with the posterior side of the paracone forming a small enamel lake at the postero-medial corner of the paracone. A posterior cingulum is present but weak. At least three roots are present, but not well preserved on any of the specimens.

The M² has a strong anterior cingulum and a weak posterior cingulum (Figure 46.2). A mesoloph is directed labially from the mure along the anterior base of the paracone. The metalophulid II connects posteriorly with the hypocone.

Czaplewski (1987) defined this genus on the basis of isolated teeth. The mandibular morphology for *Jacobsomys dailyi* can be described from the
type specimen UCMP 320578 (Figure 44.1). The massateric crest is strong and terminates anteriorly beneath the anterior root of M_1 . The dorsal and ventral branches of this crest merge beneath the posterior edge of M_1 and terminate at approximately the level of the mental foramen. The posterior edge of the diastema is very steep and the mental foramen is located dorsally. The depth of the mandible below M_1 is 3.1 (+) mm.

May (1981a) assigned this material to *Calomys* (*Bensonomys*) sp. cf. *C. gidleyi*. Following Czaplewski (1987), this material is better assigned to *Jacobsomys* and represents the earliest described species of this genus. *Jacobsomys* is further evidence of a rapid sigmodontine radiation in the late Miocene-early Pliocene in the southwestern USA. Repenning and May (1986) identified a sigmodont rodent from Blancan sediments near Truth or Consequences, New Mexico, as cf. *Oryzomys*. This material has since been referred to *Jacobsomys* sp. (Morgan and Lucas 2003), but the similarity with *Oryzomys* has led Lindsay and Czaplewski (2011) to suggest an ancestral relationship between *Jacobsomys* and *Oryzomys*.

A partial M¹ (UCMP 320594) is assigned to *J. dailyi* from locality RV-8103. The anterocone is missing, but the remainder of the tooth compares favorably with the M¹'s from locality RV-7702. Based on our interpretation of the magnetic polarity stratigraphy, RV-8103 is believed significantly younger than RV-7702 (Chron 3n.2r vs. Chron 3n.3r). *J. dailyi* may therefore extend from the latest Hemphillian into the earliest Blancan in the Horned Toad Formation pending eventual recognition of the mammal age boundary.

Order CARNIVORA Bowdich, 1821 Family CANIDAE Fischer de Waldheim, 1817 Subfamily BOROPHAGINAE Simpson, 1945

Genus BOROPHAGUS Cope, 1892

Borophagus sp., cf. B. secundus (Matthew and Cook, 1909) Figure 47

Material: UCMP 318700 – associated M^1 and left partial mandible with fragmentary P_4 - M_1 .

Localities: UCMP 318700 - RV-8102.

Description and Discussion: An associated right M^1 (Figure 47.1) and a fragmentary left mandible (Figure 47.2) represent the borophagine dog *Borophagus*. Unfortunately, the diagnostic teeth of the mandible ($P_4 - M_1$) are fragmentary. Only the roots of P_4 remain although it appears to have

been inclined posteriorly and was a relatively large tooth with an anteroposterior length of approximately 17-18 mm. Only part of the labial side of M_1 is preserved. The tooth was relatively large with an anteroposterior length of approximately 27.5 mm. M_2 is missing, but a single alveolus is present. M_3 is missing, and the alveolus is very small and slightly closed suggesting that the tooth was lost during the life of the animal.

Judging from the poorly preserved alveoli, the premolars were strongly reduced. P_1 is completely absent and P_{2-3} are represented by single, small alveoli. The alveolus for the canine is moderately large.

The reduction of both M_{2-3} and especially the premolars anterior to P_4 result in a short, stout mandible most of which was occupied by the fourth premolar, the first molar, and the canine. The tooth row is flexed labially.

The upper dentition is represented by a single M¹. The paracone is much larger than the metacone. A distinct anterolingual cingulum joins the anterior edge of the hypocone and projects anterior to the protoconule. The hypocone is well developed and is positioned directly transverse to the metacone. This specimen compares well with the M¹ assigned to *Osteoborus* cf. *cyonoides* by Webb and Perrigo (1984) from the Hemphillian Corinto Fauna of El Salvador. This species has been allocated to *Borophagus secundus* by Wang et al. (1999), an assignment that is followed here.

This material can certainly be assigned to the genus *Borophagus*. Wang et al. (1999: 296) indicate that *B. secundus* is the earliest species to show advanced features of *Borophagus*, such as a very short rostrum, broad palate, and a robust, high-crowned P_4 .

Family HEMICYONIDAE Frick, 1926 Genus AGRIOTHERIUM Wagner, 1837

cf. Agriotherium

Material: URC 18707 – edentulous fragment of right mandible, UCMP 29798 – upper premolar.

Localities: UCMP 318707 - locality RV-8105 and UCMP 29798 - locality V-2503.

Description and Discussion: A fragment of the right mandible of a large bear (UCMP 318707) contains the posterior alveolus of P_3 , both roots of P_4 , and the anterior alveolus of M_1 . UCMP 318707 compares well with USNM 264246, a nearly complete right mandible of *Agriotherium* sp. cf. *A. silva*-



FIGURE 47. 1. Borophagus cf. B. secundus (UCMP 318700), occlusal view of M^1 . SEM image. Scale equals in cm. 2. Borophagus cf. B. secundus (UCMP 318700), labial view of left dentary with fragmentary P_4 and M_1 . SEM image. Scale equals in cm.

lensis collected from the lower Coso Formation 90 miles north of the Horned Toad Hills.

Richard Tedford (AMNH, personal commun., 1980) previously assigned a single rooted, bulbous upper premolar (UCMP 29798) from the Warren Local Fauna to the genus *Agriotherium*. *Agriotherium* was also reported by Frick (1921) from the late Hemphillian Mt. Eden beds of southern California. *Agriotherium* appears to have been the common bear in the southern USA and northern Mexico during the late Hemphillian (Hunt 1998), and no reports of *Indarctos* are known from this area. Tedford et al. (2004) include *Agriotherium* as an immigrant taxon that first appears in North America in the late Hemphillian (Hh3).

Family FELIDAE Fischer de Waldheim, 1817 Subfamily MACHAIRODONTINAE Gill, 1872 Genus MACHAIRODUS Kaup, 1833

Machairodus sp. cf. M. coloradensis Cook, 1922

Material: UCMP 318701 – partial upper canine, UCMP 318702 – proximal phalanx, UCMP 318703

 - 1st metacarpal, UCMP 318704 – 4th metacarpal, UCMP 320103 – distal metacarpal, UCMP 21222 – proximal phalanx.

Localities: UCMP 318701 and UCMP 320103 – locality RV-7702; UCMP 318702 and 318704 – locality RV-8107; UCMP 318703 – locality RV-7504; UCMP 21222 – locality V-1750.

Description and Discussion: A large machairodont cat is represented in the Warren Local Fauna by a partial upper canine and five foot-elements.

Only the root portion of the upper canine was recovered and the greatest anteroposterior length of this tooth is 32.5 mm. This measurement is at the broken edge, so it is a minimum estimate. The size of this tooth compares well with measurements of canines assigned to *Machairodus coloradensis* Cook reported by Dalquest (1969) from the Coffee Ranch Local Fauna.

The foot elements of the Warren cat are also referable to M. *coloradensis* as figured by Burt (1931).



FIGURE 48. *Rhynchotherium* cf. *R. edensis* (UCMP 313449), labial view of mandible showing M_{2-3} , downward deflected symphysis, and lower tusk with enamel band. (The lower tusk is a cast of the original shown in Figure 52.) Meter stick for scale.

Martin and Schultz (1975) suggested that the holotype of Machairodus catacopis Cope was actually the pseudaelurine cat Nimravides. They recognized M. coloradensis as the only valid species of Machairodus in North America (see also Martin 1998). The large machairodont from the Coffee Ranch Quarry, commonly assigned to *M. catacopis* (Dalquest 1969), is now recognized as M. coloradensis. The machairodont cat from the Warren Local Fauna is therefore assigned to M. coloradensis, as also cited by Martin (1998), who recorded this taxon in late Hemphillian faunas from the Kansas-Texas panhandle region to Arizona and California. Machairodus is not known from North American faunas younger than late late Hemphillian (Hh4) (Tedford et al. 2004).

Order URANOTHERIA McKenna and Bell, 1997

Family GOMPHOTHERIIDAE Hay, 1922 RHYNCHOTHERIUM Falconer, 1868

Rhynchotherium sp. cf. R. edensis Frick, 1921 Figures 48 – 53 Table 9

Material: Most of the material referred to this taxon represents a single individual and is given the specimen number UCMP 313449. Included are a partial palate with LM¹⁻³ and RM¹⁻³; both upper tusks; mandible with both lower tusks and LM₁₋₃, RM₂₋₃; both scapulae; left humerus; left radius; left and fragmentary right ulnas; pelvis; left femur; right tibia and fibula; left and right calcanea; right astragalus; numerous carpal-metacarpal and tarsal-metatarsal elements; axis and other miscellaneous vertebrae; and numerous ribs.

Material not assigned to this specimen includes UCMP 75438 – LM³, UCMP 316980 –

 dP_3 ?, UCMP 316979 – dP^2 ?, and LACM 121968 – deciduous lower tusk.

Localities: UCMP 313449 – locality RV-6834, UCMP 316980 – locality RC 7148, UCMP 316979 – locality RV 6834, UCMP 75438 – locality V-6638, LACM 121968 – locality LACM 1552.

Description: The unequivocal association and excellent preservation of the elements of UCMP 313449 make this a very important specimen. The nearly complete mandible (Figures 48 - 50) is relatively short with the symphyseal portion downturned at an angle of approximately 50 degrees from the plane of the tooth row. The total length of the dorsal and symphyseal furrow is 28.0 cm with an average internal width of 52.0 mm. The depth of the mandible beneath the anterior alveolus of M₁ is 14.5 cm and at the anterior edge of the ascending ramus is 11.1 cm. The greatest transverse width of the dentary is 13.0 cm just anterior to the ascending ramus. The maximum outside transverse dimension of the complete mandible near the base of the ascending rami is 34.5 cm.

The lower tusks are straight, laterally compressed, and possess a short, external enamel band (Figure 52). In detail, these two tusks are somewhat different even though they belong to the same individual (Figure 53).

The symphyseal structure of the right dentary is complete with the proximal end of the right tusk in place. The maximum observable length of the right tusk is 44.0 cm. The tusk is transversely compressed near its alveolar margin with a dorso-ventral diameter of 55.5 mm and a transverse diameter of 43.8 mm. The cross-sectional shape of the tusk changes toward the tip with a distinct flattening of the dorsal surface (Figure 53). The ventral surface of the tusk is well worn for approximately 8.0 cm



FIGURE 49. Rhynchotherium cf. R. edensis (UCMP 313449), dorsal view of symphyseal furrow. Meter stick for scale.



FIGURE 50. 1. *Rhynchotherium* cf. *R. edensis* (UCMP 313449), lingual view of left dentary with boned removed to show partially erupted M_3 . Meter stick for scale. 2. *Rhynchotherium* cf. *R. edensis* (UCMP 313449), occlusal view of left dentary with M_2 and partially erupted M_3 . Meter stick for scale.



FIGURE 51. *Rhynchotherium* cf. *R. edensis* (UCMP 313449), occlusal view of right maxillary fragment with M¹⁻² (M¹ on the right). Meter stick for scale.

from the tip. A straight enamel band extends 18.8 cm posteriorly from the tip along the external side of the tusk. This band is only 14.0 mm at its widest point and tapers slightly posteriorly where it terminates in a feathered intergrowth with the external dentinal surface. The anterior portion of the enamel band is polished by wear, but otherwise the texture is rough.

The maximum measurable length of the left lower tusk is 60.5 cm. The proximal cross-section is essentially the same as that of the right tusk with a dorso-ventral diameter of 55.4 mm and a transverse diameter of 42.2 mm (Figure 53). The distal cross-section is quite different from that of the right tusk, as there is no flattening of the dorsal surface, and the tusk comes to a more perfect point with relatively little sign of wear. The enamel band on the left tusk extends 14.2 cm posteriorly from the tip and is only 7.0 mm at its widest point. These differences suggest that the lower tusks did not share the same occlusion pattern with the upper tusks. In later species of Rhynchotherium, the lower tusks did not occlude with the upper tusks at all (Miller 1990).

The left M_1 was found near its appropriate alveolus, but at a right angle to its normal position. It appears that this tooth was near to expulsion at the time of death and fell out during burial. The tooth is extremely worn, but was originally trilophed. The right M_1 was never recovered, but

the alveoli for both of these teeth are distinct and completely open.

The M_2 's are in full occlusion with dentine apparent on all three lophids (Figure 50.2). A simple trefoil pattern is preserved on the third labial hemilophid and was presumably present on the first and second at an earlier stage of wear.

The crowns of the M_3 's are fully developed, but at the time of death, these teeth had not advanced forward into occlusion (Figures 50.1 and 50.2). Removal of bone from the internal side of the left dentary shows the posterior portion of LM₃ (Figure 50.1). This tooth has four strong lophids and an incipient fifth lophid consisting of one major and two minor conulids. Simple trefoils are present on the four major labial hemilophids. An external cingulum is present extending from the anterolabial edge of the tooth back to the base of the second lophid, beyond which the tooth is hidden.

The well preserved upper tusks are spiral with wide enamel bands extending their complete length. The right tusk is 130 cm long, and the maximum width of its enamel band is 71.5 mm. The enamel band follows the spiral of the tusk from the proximal-external side around the ventral surface to the distal-internal side.

The total length of the left tusk is 138.5 cm, and the maximum width of its enamel band is 78.6 mm. The left tusk spirals in the same sense, although symmetrically opposed to the right tusk.



FIGURE 52. *Rhynchotherium* cf. *R. edensis* (UCMP 313449), lateral view of lower tusk (distal portion) showing small enamel band (EB). Meter stick for scale.

Transverse compression at the proximal end follows the spiral of the upper tusks, but the crosssection becomes more circular distally. The maximum dimensions near the middle of the right tusk are 10.3 cm x 7.9 cm. Both tusks are slightly curved so that in a reconstructed orientation they would be curved outward in top view and concave down in side view. The enamel band of the upper tusks has a rough, pebbly texture as in the lowers, but is worn nearly smooth along the anterior third of the tusk.

The M¹'s are completely worn, but were originally trilophed (Figure 51). These teeth were presumably near to expulsion when the animal died. The M²'s are nearly in full occlusion, and the enamel of the third lophs is just barely breached (Figure 51). The first lophs are well worn so that any original trefoil pattern is now obliterated. The



FIGURE 53. *Rhynchotherium* cf. *R. edensis* (UCMP 313449), cross sections of lower tusks.

second and third lingual hemilophs exhibit a simple trefoil pattern, and the second labial hemiloph also shows an incipient trefoil. A small rugose heel projects externally from the posterior arm of the third lingual hemiloph.

The two M³'s of UCMP 313449 are completely unworn, but with wear, would exhibit simple trefoils on all four lingual hemilophs. The second labial hemiloph would also develop a trefoil pattern with moderate wear. The trefoil pattern of the fourth internal hemiloph of UCMP 75438 is less well developed than in UCMP 313449. Both specimens exhibit a small rugose heel projecting labially from the posterior extension of the fourth lingual hemiloph.

TABLE 9. Measurements of *Rhynchotherium* sp. cf. *R.*edensis (UCMP 313449) Maximum dimensions in mm.

Tooth	A.P.	т
RM ¹ very worn	79.0	65.0
LM ¹ very worn	82.0	66.0
RM ² moderately worn	119.0	80.0
LM ² moderately worn	112.0	79.0
LM ³ unworn	160.0	84.0
LM ₁ very worn	87.0	58.0
LM ₂ moderately worn	115.0	72.0
RM ₂ moderately worn	112.0	72.0
LM ₃ unworn	175.0	75.0

LACM 129168 is a very small and presumably deciduous lower tusk. The tusk is transversely compressed and curves upward (?). Its slight lateral curvature suggests that it was from the right dentary and, therefore, the external surface is best preserved. There is no trace of an enamel band. Numerous longitudinal ridges extend down the tusk resembling the "corduroy" texture described by Olsen (1957). The post-cranial material of UCMP 313449 is not described. These specimens are mounted in the Geology Department at U.C. Riverside.

Discussion: May (1981a) originally assigned the gomphotheriid mastodont from the Warren Local Fauna to the genus Cuvieronius, based on his assessment that Rhynchotherium was nomen dubium. Nearly every author who has described Rhynchotherium and/or Cuvieronius fossils argues that the taxonomic history of these genera is both confusing and complicated (Miller 1980; Webb and Perrigo 1984; Miller 1990; Lambert 1996; Corona-M and Alberdi 2006). However, most authors continue to use these generic names and Lambert and Shoshani (1998) diagnose Rhynchotherium as having variably spiral upper tusks with enamel bands; lower tusks that are medio-laterally compressed and commonly have enamel bands; and mandibular symphysis longirostrine, but significantly deflected downward. They characterize Cuvieronius as brevirostrine and lacking lower tusks, but sharing the characters of spiral upper tusks with enamel bands and molar morphology with *Rhynchotherium*. The gomphotheriid material from the Warren Local Fauna is assignable to the genus Rhynchotherium on the basis of its spiral upper tusks with enamel bands, relatively simple molars, mandible with downturned symphysis, and laterally compressed lower tusks with external enamel bands. The material compares reasonably well with R. edensis from Mt. Eden (Frick 1933). However, the enamel bands on the lower tusks are quite reduced with respect to R. edensis. The Warren material is therefore referred to as Rhynchotherium sp. cf. R. edensis.

The molar morphology of these gomphotheriid taxa exhibit large variability, and specific characteristics are unclear. *R*. sp. cf. *R. edensis* does possess a pentalophid on M_3 consisting of three conulids like *R. edensis*. *R. falconeri* reportedly has two conulids in this position, and *R. browni* only has a single conulid. The significance of this variability is not clear.

The upper tusks of UCMP 313449 are spiral with a wide enamel band. Miller (1980) also reports

a similar upper tusk from the early Blancan, Las Tunas fauna of Baja, California. The only completely observable M_3 of R. sp. cf. R. edensis has three conulids forming the posterior heel and a length-width index of 43. Both of these parameters compare well with topotypic R. edensis. Webb and Tessman (1968) and Miller (1980) use these criteria to separate species, but it remains unclear whether these characters are diagnostic of different species.

The lower tusks of UCMP 313449 are laterally compressed as in R. edensis, but the external enamel band on these tusks is much narrower and shorter. Believing the Warren Local Fauna to be older than Mt. Eden, May and Repenning (1982) suggested that the reduced enamel band on the Warren Rhynchotherium (their Cuvieronius), represented a more primitive condition. Webb and Perrigo (1984) disagreed with this hypothesis as material assigned to R. blicki from the late Clarendonian to early Hemphillian Gracias Fauna of Honduras possess laterally compressed lower tusks with a broad enamel band. Furthermore, these authors disagree with the assignment of the Mt. Eden gomphotheriid to Cuvieronius, as they believe this genus is characterized by the lack of lower tusks. They suggest that the New World gomphotheres evolved from longirostrines by deflection of the symphysis, then by shortening and thickening the mandible and finally by losing the lower tusks. The reduced enamel band in R. sp. cf. R. edensis from Warren might therefore be more derived than R. edensis from Mt. Eden, however the neotype of the latter figured by Frick (1933) appears to be more brevirostrine with a symphyseal angle of approximately 60° rather than the 50° observed in the Warren form. The symphyseal angle of the more primitive R. blicki from the Gracias Fauna is reported by Webb and Perrigo (1984) as approximately 25°, however, based on their figure 4, the angle measured relative to the tooth row appears to be closer to 40°.

Rhynchotherium sp. cf. *R. edensis* also compares favorably with *R.* cf. *R. falconeri* described by Miller (1980) from the early Blancan Las Tunas Local Fauna (Baja, California). This form has a continuous enamel band on the lower tusks that is narrower than in *R. edensis* (20 mm vs. 31 mm), but has a less abbreviated mandible and a symphyseal angle of 56°. As described above, the enamel band on the lower tusks of *R.* sp. cf. *R. edensis* is 7-14 mm wide and only present on the distal half of the tusk. Miller (1980) suggested that *R. edensis*, *R. falconeri*, and *R. browni* may all rep-



FIGURE 54. Pliomastodon vexillarius (UCMP 318112), oblique view of M₃, anterior to the right. Scale in inches.

resent a single species, but he did not formally propose synonymy.

Miller (1990) described a skull and mandible of Rhynchotherium from the Gila River area of southeastern Arizona that he believes is probably latest Pliocene in age. Unfortunately, the specimen was collected without locality information so the stratigraphic provenance and age is uncertain. Nevertheless, this specimen possesses lower tusks that lack enamel bands in a brevirostrine mandible with a strongly deflected symphysis (65°). Unlike older specimens of Rhyncotherium that possess enamel bands on the lower tusks, the upper and lower tusks of the Gila River Rhynchotherium never came into occlusion. Miller (1990) suggested a probable phylogeny progressing from Gomphotherium to Rhynchotherium to Cuvieronius.

Family MAMMUTIDAE Hay, 1922 Genus PLIOMASTODON Osborn, 1926

Pliomastodon vexillarius Matthew, 1930 Figures 54, 55

Material: UCMP 318112 – associated LM_2 , LM_3 , RM_3 ; UCMP 318113 – fragmentary right mandible with partial M_3 ; UCMP 318115 – fragmentary left mandible with M_3 ; UCMP 320613 – partial LM_2 ; UCMP 31814 – P_4 ; UCMP 320614 – magnum.

Localities: UCMP 318112 – locality RV 8126, UCMP 318113 – locality RV 7148, UCMP 318114 – locality RV 8112, UCMP 318115 – locality RV 8128, UCMP 320613 – locality RV 8114, UCMP 320614 – locality RV 7702.

Description and Discussion: A second proboscidean is represented in the Warren Local Fauna by six specimens, most of which are teeth. A moderately well worn, left M_2 (UCMP 318115) is trilophid with clean valleys and lacks accessory conulids on the lophids. Anterior and posterior cingula are present, but these are small and without accessory conulids. The tooth widens posteriorly.

The associated left and right M_3 's (UCMP 318112) (Figure 54) have four complete lophids and small fifth lophids. The latter consist of two major conulids with a small posterior projection and are removed from the fourth complete lophid by a deep valley. The length-width index for each of these unworn teeth is 44.

In contrast, the M_3 of UCMP 38115 (Figure 55) has a posterior heel developed as a narrow ridge with five to six small conulids. This heel is also much closer to the fourth major lophid causing the tooth to appear relatively wider than UCMP 318112. This qualitative appearance is quantitatively expressed as the greater width-length index of 53. The valleys lack accessory conulids and are partially filled with cement.



FIGURE 55. *Pliomastodon vexillarius* (UCMP 318115), oblique view of partial left dentary with M₃. Note the smaller and more compressed posterior heel (at right) in this specimen as compared to that in Figure 54. Specimen approximately same size as UCMP 318112.

A moderately worn right P_4 (UCMP 318114) is bilophid with strong anterior and posterior cingula that are ornamented with small accessory conulids.

The anterior portion of a left mandible is preserved on UCMP 318115 with no suggestion of an alveolus for a lower tusk.

Madden (1977, 1980) has presented brief reviews of *Pliomastodon* concluding that there are only two valid species in North America, namely P. matthewi and P. vexillarius. Madden (1980) states "... (late Hemphillian to late Blancan) P. vexillarius is distinguished from progenitor P. matthewi by its rounded upper tusks, tuskless mandibles, and 4-5 ridged M₃." The material from the Warren Local Fauna is consistent with this diagnosis of P. vexillarius. The M₃'s of UCMP 318112 are quite advanced with a well developed pentalophid and a low width-length index. The seeming disparity between these M₃'s and UCMP 318115 is attributed to either sexual dimorphism or a large normal interspecific variation. Lambert and Shoshani (1998) consider Pliomastodon Osborn (1926) to be a junior synonym of Mammut Blumenbach (1799), and they include only two valid species: M. americanum and M. matthewi. Mammut vexillarius (misspelled vexillanus on p. 610 of Lambert and Shoshani 1998) is assigned to Mammut sp. along with all other named species. These authors suggest that Mammut extends from the Clarendonian to the terminal Pleistocene and was uncommon yet

widespread across North America during the Clarendonian and Hemphillian "where it is commonly referred to as *Pliomastodon* in the literature." We have followed this practice, using the name *Pliomastodon*.

> Order PERISSODACTYLA Owen, 1848 Family EQUIDAE Gray, 1821

Genus DINOHIPPUS Quinn, 1955 (synonym: PLIOHIPPUS, in part) Dinohippus edensis Frick, 1921 Figure 56

Table 10

Material: UCMP 29778 – right mandible fragment with P_2 - P_4 , UCMP 29785 – right mandible fragment with P_4 - M_3 , UCMP 320010 – right mandible fragment with partial P_2 - M_3 , UCMP 320050 – left mandible fragment with P_2 - M_1 , UCMP 320011 – left mandible fragment, UCMP 320052 – partial symphysis, UCMP 320057 – symphysis with left and right I₁₋₃, UCMP 320058 P_3 ?, UCMP 320054 – P_4 ?, UCMP 320048 – P_3 , UCMP 320016 – M_3 , UCMP 320015 – DP₂?, UCMP 320019 – P_4 , UCMP 320017 – M_2 , UCMP 29787 – M_3 , UCMP 320014 – associated P_3 and DP₄?, UCMP 320018 – P_3 , UCMP 320049 – M_3 , UCMP 320013 – P_3 , UCMP 320012 – P_2 , UCMP 320051 – associated P_3 and P_4 , UCMP 320053 – M_1 , UCMP 320055 –



FIGURE 56. 1. *Dinohippus edensis*, (UCMP 320023), occlusal view of P⁴. Scale in cm. 2. *Dinohippus edensis*, (UCMP 320023), lateral view of P⁴. Scale in cm. 3. *Dinohippus edensis*, (UCMP 320020), occlusal view of P⁴. Scale in cm. 4. *Dinohippus edensis*, (UCMP 320020), lateral; view of P⁴. Scale in cm. 5. *Dinohippus edensis*, (UCMP 329785), occlusal view of right dentary with P₄ - M₃. Note isolated lake on M₃ (at left). Scale in cm.

DP₃?, UCMP 320056 - M₃, UCMP 29775 - P₂, UCMP 320060 - M1, UCMP 320061 - M2, UCMP 29784 - M², UCMP 320043 - M¹or², UCMP 320025 – P², UCMP 320045 – upper cheek tooth, UCMP 320034 - P⁴ or M¹, UCMP 320046 - M², UCMP 320038 - P⁴, UCMP 320035 - M¹, UCMP 320044 - P⁴, UCMP 320040 - two unworn upper cheek teeth, UCMP 320031 - M², UCMP 320598 -P4, UCMP 320022 - P4, UCMP 320033 - M1, UCMP 320030 - M³, UCMP 320039 - unworn upper cheek tooth, UCMP 320032 - P4, UCMP 29781 - P³, UCMP 320026 - P³, UCMP 320027 -P⁴?, UCMP 320037 - P², UCMP 320042 - M¹, UCMP 320020 - P⁴, UCMP 29784 - M³, P², M¹?, UCMP 29775 - M¹?, P², UCMP 320028 - P⁴, UCMP 320029 - P2, UCMP 320047 - P2?, UCMP 320041 - M³, UCMP 123628 - M³, UCMP 320059 - left and right P², UCMP 320021 - P², UCMP 320063 - medial phalanx, UCMP 320064 - distal metapodial, UCMP 320065 - proximal phalanx,

UCMP 320066 – 2nd or 4th proximal metapodial (splint), UCMP 320067 – astragalus, UCMP 320068 – astragalus, UCMP 320069 – astragalus, UCMP 320070 – astragalus, UCMP 320071 – calcaneus, UCMP 320073 – navicular, UCMP 320076 – medial phalanx, UCMP 320077 – 3rd metapodial, UCMP 320078 – medial phalanx, UCMP 320079 – medial phalanx, UCMP 320080 – distal phalanx, UCMP 320081 – distal 3rd metapodial, UCMP 320082 – medial phalanx, UCMP 320083 – medial phalanx, UCMP 320084 – proximal phalanx, UCMP 320083 – medial phalanx, UCMP 320084 – proximal phalanx, UCMP 320085 – proximal phalanx, UCMP 320086 – 3rd metapodial, UCMP 320087 – scaphoid.

Localities: UCMP 29778 – locality V2503, UCMP 29785 – locality V-2503, UCMP 320010 – RV-8125, UCMP 320050 – locality RV-8110, UCMP 320011 – locality RV-8112, UCMP 320052 – locality RV-7702, UCMP 320057 – locality RV-8113, UCMP 320058 – locality RV-8114, UCMP 320054

oth	Ν	0.R.	х	S.D.
L	4	28.0-30.8	29.0	1.3
W	4	15.0-17.7	16.2	1.2
L	6	24.0-28.8	26.3	1.7
W	6	15.1-18.0	17.2	1.0
L	5	22.9-25.3	24.2	1.2
W	5	16.1-18.0	17.2	1.0
L	5	17.9-24.5	20.8	2.4
W	5	14.5-16.0	15.5	0.6
L	4	21.1-24.1	22.4	1.2
W	4	11.5-15.1	13.7	1.5
L	3	25.1-29.0	26.7	2.0
W	2	12.1-13.7	12.9	1.1
L	3	32.1-33.7	32.8	0.8
W	4	22.6-25.3	23.7	1.2
Prot	1	7.3		
L	2	23.6-26.7	25.2	2.2
W	2	25.0-28.5	26.8	2.5
Prot	2	7.7-7.8	7.75	0.07
L	4	24.4-26.4	25.5	1.0
W	4	25.3-27.7	26.3	1.0
Prot	3	6.2-7.8	7.3	0.09
L	2	19.8-24.4	22.1	3.3
W	2	24.6-25.5	25.1	0.6
Prot	3	6.9-7.9	7.4	0.5
L	2	23.1-23.8	23.5	0.8
W	1	24.3		
Prot	2	7.1-8.2	7.7	0.8
L	5	23.2-27.2	24.9	2.0
W	5	20.6-24.9	23.0	1.6
Prot	3	7.8-8.8		
	Poth L W L W L W L W L W L W U V V Prot L W Prot L W Prot L W Prot L W Prot L W Prot L W Prot L W Prot L W	L4W4L6W6L5W5L3W4L3W2L3W2Prot1L2W2Prot3U2Prot3L2W2Prot3L2W2Prot3L2W1Prot3L2W1Prot3L2W1Prot3L5W5	N O.R. L 4 28.0-30.8 W 4 15.0-17.7 L 6 24.0-28.8 W 6 15.1-18.0 L 5 22.9-25.3 W 5 16.1-18.0 L 5 17.9-24.5 W 5 14.5-16.0 L 4 21.1-24.1 W 4 11.5-15.1 L 3 25.1-29.0 W 2 12.1-13.7 L 3 32.1-33.7 W 4 22.6-25.3 Prot 1 7.3 L 2 23.6-26.7 W 2 25.0-28.5 Prot 1 7.3 L 2 23.6-26.7 W 2 25.3-27.7 W 2 25.3-27.7 Prot 3 6.2-7.8 L 2 19.8-24.4 W 2 <t< td=""><td>N O.R. X L 4 28.0-30.8 29.0 W 4 15.0-17.7 16.2 L 6 24.0-28.8 26.3 W 6 15.1-18.0 17.2 L 5 22.9-25.3 24.2 W 5 16.1-18.0 17.2 L 5 17.9-24.5 20.8 W 5 14.5-16.0 15.5 L 4 21.1-24.1 22.4 W 4 11.5-15.1 13.7 L 3 25.1-29.0 26.7 W 2 12.1-13.7 12.9 L 3 32.1-33.7 32.8 W 4 22.6-25.3 23.7 Prot 1 7.3 1 L 2 23.6-26.7 25.2 W 2 25.0-28.5 26.8 Prot 2 7.7-7.8 7.75 L 4 24.</td></t<>	N O.R. X L 4 28.0-30.8 29.0 W 4 15.0-17.7 16.2 L 6 24.0-28.8 26.3 W 6 15.1-18.0 17.2 L 5 22.9-25.3 24.2 W 5 16.1-18.0 17.2 L 5 17.9-24.5 20.8 W 5 14.5-16.0 15.5 L 4 21.1-24.1 22.4 W 4 11.5-15.1 13.7 L 3 25.1-29.0 26.7 W 2 12.1-13.7 12.9 L 3 32.1-33.7 32.8 W 4 22.6-25.3 23.7 Prot 1 7.3 1 L 2 23.6-26.7 25.2 W 2 25.0-28.5 26.8 Prot 2 7.7-7.8 7.75 L 4 24.

TABLE 10. Measurements of *Dinohippus edensis*. Dimensions in mm.

locality RV-7148, UCMP 320048 – locality RV-8115, UCMP 320016 – locality RV-8115, UCMP 320015 – locality RV-8107, UCMP 320019 – locality RV-8105, UCMP 320017 – locality RV-8110, UCMP 29787 – locality V-2503, UCMP 320014 – locality RV-8117, UCMP 320018 - RV-8107, UCMP 320049 – locality RV-8125, UCMP 320013 – locality RV-6834, UCMP 320012 – locality RV-8118,

UCMP 320051 - locality RV-8120, UCMP 320053 - locality RV-7702, UCMP 320055 - locality RV-8114, UCMP 320056 - locality RV-8105, UCMP 29775 - locality V-2503, UCMP 320060 - locality RV-8126, UCMP 320061 - locality RV-8126, UCMP 29784 - locality RV-2503, UCMP 320043 locality RV-6834, UCMP 320046 - locality RV-7702, UCMP 320038 - locality RV-7702, UCMP 320035 - locality RV-8114, UCMP 320044 - locality RV-8107, UCMP 320040 - locality RV-8110, UCMP 320031 - locality RV-6834, UCMP 320598 - locality RV-7702, UCMP 320022 - locality RV-8127, UCMP 320033 - locality RV-8105, UCMP 320030 - locality RV-8112, UCMP 320039 - locality RV-8110, UCMP 320024 - locality RV-7702, UCMP 320036 - locality RV-8107, UCMP 320032 - locality RV-7702, UCMP 320023 - locality RV-8107, UCMP 29781 - locality V-2503, UCMP 320026 - locality RV-8114, UCMP 320027 - locality RV-8121, UCMP 320037 - locality RV-8110, UCMP 320042 - locality RV-8110, UCMP 320020 - locality RV-7148, UCMP 29775 - locality V-2503, UCMP 320028 - locality RV-8107, UCMP 320029 - locality RV-8107, UCMP 320047 - locality RV-7702, UCMP 320041 - locality RV-8105, UCMP 123628 - locality V-6638, UCMP 320059 - locality RV-8105, UCMP 320021 - locality RV-8126, UCMP 320063 - locality RV-8126, UCMP 320064 - locality RV-8126, UCMP 320065 - locality RV-8126, UCMP 320066 - locality RV-8126, UCMP 320067 - locality RV-8105, UCMP 320068 - locality RV-8125, UCMP 320069 - locality RV-8122, UCMP 320070 - locality RV-8107, UCMP 320071 - locality RV-7702, UCMP 320073 - locality RV-8123, UCMP 320076 - locality RV-8110, UCMP 320077 - locality RV-7702, UCMP 320078 - locality RV-8124, UCMP 320079 - locality RV-8105, UCMP 320080 - locality RV-8120, UCMP 320081 - locality RV-7702, UCMP 320082 - locality RV-M799, UCMP 320083 - locality RV-7702, UCMP 32084 - locality RV-8120, UCMP 320085 - locality RV-7702, UCMP 320086 - locality RV-7702.

Description and Discussion: A single horse from the Warren Local Fauna is represented predominantly by isolated teeth and post-cranial material. Four partial mandibles contain associated lower teeth. However, no cranial specimens have been recovered. This material compares favorably with *Dinohippus edensis* Frick from the late Hemphillian Mt. Eden Local Fauna in California. Measurements of the cheek teeth are shown in Table 10. The Warren horse is similar in size to *Dinohippus edensis*, *D. osborni*, *D. mexicanus* and *D. interpolatus*. The upper cheek teeth are slightly to moderately curved, similar to *D. mexicanus* or *D. osborni*, but less than *D. interpolatus* (Figure 56). The protocone is generally oval in shape with no lingual groove and no anterior projection. The pre-protoconal groove is shallow and projects externally toward the area between the mesostyle and metastyle. These characters of the protocone are considered primitive and distinguish the Warren horse from both *D. mexicanus* and *D. osborni*. Large samples of *D. interpolatus* exhibit variation in protocone shape from the primitive condition similar to *D. edensis*, to some with an incipient anterior projection.

The fossette borders of the upper molars exhibit simple plications including a pli-protoloph which become obliterated with extended wear. A pli-caballin is present on the premolars but absent on the molars, as generally common in Neogene equids. The styles are moderately developed as in *D. edensis* but smaller than *D. mexicanus*.

The lower premolars are considerably larger than the molars (Figure 56.5). The metaconid is slightly larger than the metastylid although more nearly equal than in the molars. The metastylid of P_2 is much larger than the metaconid. The entoconid is relatively large and round to oval in shape. The entoflexid is well developed with strong anterior and posterior projections while the metaflexid has only a slight anterior projection on P_2 and only posterior projections on P_3 and P_4 . The labial walls of the protoconid and hypoconid are rounded as in *D. edensis* rather than flattened as in *D. mexicanus*.

In the lower molars, the metaconid is much larger than the metastylid with only a very shallow lingual valley separating these cusps. The labial reentrant projects lingually between the entoflexid and the metaflexid. A pli-caballinid is never present. In two of the six M_3 's, the posterior enamel loop is completely isolated as a lake (Figure 53.5), a condition that does not appear to be a result of wear as other specimens (at comparable wear stages) show a joined posterior loop.

The horse from the Warren Local Fauna is similar in size to *D. edensis*, *D. osborni*, *D. mexicanus*, and *D. interpolatus*. It differs from *D. mexicanus* in having a more primitive protocone, less complex fossette borders, weaker styles, rounded labial walls on the protoconids and hypoconids and a better developed linguaflexid (MacFadden 1984). It differs from *D. interpolatus* in having less curved upper cheek teeth and in never exhibiting an

advanced protocone. It differs from *D. osborni* in having a more primitive protocone.

Lance (1950) suggested that the variation seen in the large sample of *D. mexicanus* from the Yepom,era was as great as the differences described by Frick (1921) in separating *D. osborni* from *D. edensis*. A major distinction between these two species is the stage of development of the protocone. MacFadden (1998) recognized both *D. osborni* and *D. edensis* as valid species of *Dinohippus*. The horse from the Warren Local Fauna resembles *D. edensis* very favorably but never exhibits the derived protocone of *D. osborni*.

Family RHINOCEROTIDAE Gray, 1821

Subfamily RHINOCEROTINAE Gray, 1821 Genus TELEOCERAS Hatcher, 1894

Teleoceras sp. cf. *T. fossiger* Cope, 1915 Figure 57

Material: UCMP 318705 – left P^2 , UCMP 316981 – left M_1 ?, UCMP 29797 – metapodial.

Localities: UCMP 318705 - locality RV-8114, UCMP 316981 - locality RV-7702, UCMP 29797 - locality V-2503.

Description and Discussion: Three specimens from the Warren Local Fauna are identified as the rhino *Teleoceras* Hatcher. The most diagnostic of these is a well worn, partially fragmented, left P² (Figure 57.3). It compares favorably with *Teleoceras fossiger* from Long Island, Kansas, and with the *T. fossiger* from Long Island, Kansas, and with the *T. fossiger* skull figured by Matthew (1932) from Brown County, Nebraska. It is also similar to the P² of *T.* cf. *fossiger* figured by Stirton (1939) from the Pinole Tuff Local Fauna, California.

The M_1 ? is extremely worn although it is consistent with the size of *T. fossiger*. A single metapodial is referable to *Teleoceras* (Figure 54.1 and 54.2).

The fragments of rhino material from the Warren Local Fauna preclude more detailed discussion of specific relationships: it appears most similar to *T. fossiger* from Hemphillian deposits in California and the Great Plains. Tanner (1975) has emphasized the evolutionary increase in size from the Valentinian *Teleoceras* sp. (Skinner et al., 1968) to *T. schultzi* Tanner from the late Hemphillian. However, Prothero (2005) suggested that *T. fossiger* is restricted to the early Hemphillian, and late Hemphillian forms of this genus are smaller. The few specimens from the Warren Local Fauna are within the known size range of Hemphillian forms.



FIGURE 57. 1. *Teleoceras* cf. *T. fossiger* (UCMP 29797), dorsal view of metapodial. Scale in cm. 2. *Teleoceras* cf. *T. fossiger* (UCMP 29797), lateral view of metapodial. Scale in cm. 3. *Teleoceras* cf. *T. fossiger* (UCMP 318705), occlusal view of fragmentary P². Scale in cm.

Order ARTIODACTYLA Owen, 1848 Family TAYASSUIDAE Palmer, 1897 Genus PROSTHENNOPS Gidley, 1904

cf. Prosthennops sp.

Material: UCMP 318706 – upper canine, UCMP 29799 – astragalus

Localities: UCMP 318706 – locality RV-6834, UCMP 29799 - locality V-2503.

Description and Discussion: The peccary *Prosthennops* Gidley is questionably represented by an upper canine and an astragalus. The canine compares favorably with *Prosthennops kernensis* from the Kern River Formation of California. Wright (1998) lists *Prosthennops kernensis* among a group of indeterminate Neogene tayassuids.

Family CAMELIDAE Gray, 1821 Subfamily CAMELINAE Gray, 1821 Genus MEGATYLOPUS Matthew and Cook, 1909

Megatylopus cf. M. matthewi Webb, 1965 Figures 58, 59 Table 11

Material: UCMP 320090 – distal metapodial, UCMP 320091 – unciform, UCMP 320092 – right mandible fragment with partial M3, UCMP 320093 – right mandible fragment with partial M_3 , UCMP 320094 – left maxillary fragment with M¹⁻³, UCMP 320095 – left M², UCMP 320096 – astragalus, UCMP 320098 – proximal phalanx, UCMP 29790 – caniniform tooth, UCMP 29788 – ulna (proximal end), trapezoid, cuboid, cuneiform, lunar, and four distal metapodial fragments, LACM 1552 – fibula.

Localities: UCMP 320090 – locality RV-8110, UCMP 320091 – locality RV-6834, UCMP 320092 – locality RV-8107, UCMP 320093 – locality RV-8129, UCMP 320094 – locality RV-8107, UCMP 320095 – locality RV-8112, UCMP 320096 – locality RV-7702, UCMP 320098 – locality RV-8107, UCMP 29788 – locality V2503, UCMP 29790 – locality V-2503, LACM 1552 – locality LACM 1552.

Description and Discussion: A very large camel is present in the Warren Local Fauna but is represented by limited material. UCMP 320094 (maxillary with M¹⁻³, Figure 59) represents an old individual with M¹ completely worn and M³ moderately worn. The parastyle and mesostyle of M³ are well developed as is a strong anterolabial rib.

Entostyles are absent on all three upper molars as well as on UCMP 320095 (M^2), although small cingula are present on both sides of the valley between the protocone and the metaconule near the base of the enamel. Both M_3 's lack anterior stylids.

Harrison (1985) grouped the large camels *Megatylopus* and *Titanotylopus* together in the Tribe Camelini united primarily by a series of man-



FIGURE 58. Above: (UCMP 320611) *Hemiauchenia vera* metapodial lacking the distal condyles. Below: (UCMP 320090) *Megatylopus* cf. *M. matthewi*, fragmentary distal metapodial. Scale in cm.



FIGURE 59. (UCMP 320094) *Megatylopus* cf. *M. matthewi*, occlusal view of maxillary fragment with M¹⁻³ (left to right in photo). Scale in cm.

dibular and cranial features. Very little of the material from the Warren Local Fauna provides diagnostic evidence for separation of these two taxa. *Titanotylopus* is generally considered to have less hypsodont cheek teeth and larger body size than *Megatylopus*. In his review of *Megatylopus*, Webb (1965) recognized four species that are diagnosed primarily on premolar characters and cranial morphology. However, Harrison (1985) recognized only two valid species (*M. gigas* and *M. matthewi*) distinguished by P₃ morphology and the depth of the maxillary fossa. The holotype of *Megatylopus matthewi* from the late Hemphillian Coffee Ranch Local Fauna compares favorably with UCMP 320094. This comparison includes overall size, as well as dental morphology. Webb (1965) states that the upper molars are of little diagnostic value, however, he describes *M. matthewi* as having well developed parastyles, mesostyles, and anterolabial ribs, all of which are observed in the Warren *Megatylopus*. *Megatylopus* ranges from the late Clarendonian to the early Blancan in the **TABLE 11.** Measurements of *Megatylopus* cf. *M. matthewi.* Dimensions in mm.

Specimen	A.P. Length	
UCMP 320092 M ₃	55.5	
UCMP 320093 M ₃	57.0	
UCMP 320094 M ¹⁻³	112 (+)	

western USA and *M. matthewi* has been described from the Hemphillian Wikieup Local Fauna, Arizona, the Chamita Formation, New Mexico, and the El Ocote Local Fauna, Mexico.

Genus HEMIAUCHENIA Gervais and Ameghino, 1880

Hemiauchenia vera Matthew, 1909 Figures 58, 60 Table 12

Material: UCMP 320612 – right and left mandibles, and partial maxillary; UCMP 320611 – metapodial; UCMP 29794 – right mandible fragment with P_4 - M_2 and roots of P_3 ; UCMP 320126 – proximal phalanx; UCMP 320127 – distal end of proximal phalanx; UCMP 320117 – unworn upper molar; UCMP 320121 – partial upper molar; UCMP 320124 –

TABLE 12. Measurements of *Hemiauchenia vera*. Dimensions in mm.

Specimen	A.P. Length
UCMP 320612 P ₃ -M ₃	120.0
UCMP 320612 M ₁₋₃	84.0
UCMP 320612 P ⁴ -M ³	92.0
UCMP 320612 M ¹⁻³	77.0
UCMP 329794 P ₄	14.9
UCMP 329794 M ₁	20.2
UCMP 329794 M ₂	26.9

astragalus; UCMP 29791 – astragalus; UCMP 320131 – partial lower molar.

Localities: UCMP 320612, and UCMP 320131 – locality RV-8129; UCMP 320611 and UCMP 320117 – locality RV-6834; UCMP 320126 and UCMP 320121 – locality RV-7702; UCMP 320124 – locality RV-8112; UCMP 320127 – locality RV-8114; UCMP 29794 and UCMP 29791 – locality V-2503.

Description and Discussion: A medium size, lamine camel in the Warren Local Fauna is identified as *Hemiauchenia vera* Matthew. The best



FIGURE 60. 1. *Hemiauchenia vera* (UCMP 320612), labial view of right dentary. Scale in cm. 2. *Hemiauchenia vera* (UCMP 320612), occlusal view of partial maxilla with P⁴ - M³ (left to right). Scale in cm.

specimen, UCMP 320612 (Figure 60), includes associated left and right mandibles and the left maxillary of an advanced juvenile with P_3 just erupting, C_1 in the process of being replaced, and three alveoli of dP_4 still present. The right mandible is nearly complete except for fragmentary dentition. The anterior portion of the left mandible is missing. UCMP 29794 is a fragmentary right mandible with P_4 - M_2 of a mature adult. The lower dental formula of this taxon is I_{1-3} , C_1 , $P_{1, 3, 4}$, and M_{1-3} . The lower molars are relatively low crowned, reflected in the shallow depth of the mandible.

Diagnostic characters of the lower dentition include the small canine, the lack of a P_2 , the length of the P_{1-3} diastema (40 mm), the morphology of P_4 , and the moderately strong anterior stylids ("Ilama buttresses") on M_2 and M_3 . The P_4 of UCMP 29794 is angular with a single posterior fossetid and a strong anterolingual groove. These characters, along with the sharp diastemal crest and the long slender metapodial (UCMP 320611), permit confident assignment to the genus *Hemiauchenia*.

The P_4 - M_3 length is difficult to assess accurately because the M_3 is absent on UCMP 29794, and the permanent P_4 is absent on UCMP 320612. The size of the Warren *Hemiauchenia* appears to be slightly larger than the holotype of *H. vera*, although measurements of individual teeth (e.g., M_2) are very similar.

The upper dentition is best represented by a maxillary (UCMP 320612) with P⁴-M³ (Figure 60.2). The permanent P⁴ has erupted but is essentially unworn, as is the M³. Parastyles and mesosyles are relatively strong with moderately developed external ribs. Entostyles are absent.

Breyer (1977) reviewed the genus *Hemi-auchenia* and recognized three North American species including *H. vera*, *H. blancoensis*, and *H. macrophela*. Breyer concluded that these three species can be separated based on the post-P₁ diastemal length, with post-P₁ diastemal length of 35 mm in the holotype of H. vera, 50 mm in *H. blancoensis*, and 60 mm in *H. macrophela* (Breyer 1977). The latter two species are known from Blancan and Pleistocene faunas of North America, respectively. Post-P₁ diastemal length in the Warren Hemiauchenia is 40 mm, placing it in *H. vera*.

Honey et al. (1998) continued to recognize these three species and follow the suggestion of Webb (1974) that *Tanupolama* is a junior synonym of Hemiauchenia, and Webb et al. (1981) that "*H*."

minima from Florida (Mixon Bone Bed and Love Local Faunas) deserves a new generic name.

The primitive hypsodonty, the shallowness of the mandible, the moderate development of the anterior stylids on M_{2-3} , the short post-P₁ diastema, and the retention of P₃ allow taxonomic assignment of the Warren lamine to *Hemiauchenia vera*. *H. vera* is known from Hemphillian faunas of North America including the Ogallala Group near Long Island, Kansas; Coffee Ranch Local Fauna, Texas; Bone Valley, Florida; San Juan – Rak Camel Quarries Horizon of the Chamita Formation, New Mexico; Wikieup Local Fauna, Arizona; Yerrington, Nevada and the Modesto Reservoir Local Fauna, California.

CAMELIDAE

gen. et. sp. indet. Figure 61 Table 13

Material: UCMP 320110 – right mandible with P₄-M₃; UCMP 320089 – left maxilla with M¹⁻³; UCMP 320115 – M₃; UCMP 320113 – M₂; UCMP 320088 – M²; UCMP 320114 – lower molar; UCMP 320127 – upper molar; UCMP 320119 – M²; UCMP 320120 – M³; UCMP 320116 – maxilla fragment with M¹⁻²; UCMP 320123 – astragalus; UCMP 29795 – astragalus; UCMP 320118 – P⁴.

Localities: UCMP 320110 and UCMP 320089 – locality RV-8129, UCMP 320115 and UCMP 320118 – locality RV-8114, UCMP 320113 and UCMP 320123 – locality RV-6834, UCMP 320088 and UCMP 320120 – locality RV-7148, UCMP 320114 and UCMP 320127 – locality RV-7702, UCMP 320119 – locality RV-8121, UCMP 29795 – locality V-2503.

Description and Discussion: A third camelid of uncertain identity is present in the Warren Local Fauna. UCMP 320110 (Figure 61) is a nearly complete right mandible extending from the posterior edge of the symphysis to the base of the ascending ramus with P_4 - M_3 and no alveoli for P_2 or P_3 . The diastemal crest is not as sharp as in Hemiauchenia vera. The absence of P_3 is an advanced character observed in Camelops, Lama, and Camelus although Webb (1974) notes that the presof P_3 is variable in Pleistocene ence Hemiauchenia. The teeth are well worn, and no fossetid is observable on P₄. This tooth differs from that of the larger Hemiauchenia vera by being less angular with a weaker anterolingual groove. The M₁ is worn nearly to the base of the enamel and is



FIGURE 61. 1. Camelidae gen. et. sp. indet. (UCMP 320089), occlusal view of left maxillary fragment with M^{1-3} (left to right). Scale in cm. 2. Camelidae gen. et. sp. indet. (UCMP 320110), labial view of right dentary with $P_4 - M_3$. Scale in cm. 3. Camelidae gen. et. sp. indet. (UCMP 320110), occlusal view of right dentary with $P_4 - M_3$. Scale in cm.

of little diagnostic value. Anterior stylids are absent on all lower molars of these specimens except for UCMP 320115, a lower M_3 with a weak anterolingual stylid that is referred to this taxon on the basis of size. The upper molars are undiagnostic except for their relatively low height of crown (Figure 61.1).

Following Harrison (1979), only one genus belonging to the subfamily Camelini has P_2 and P_3 absent and also lacks anterior stylids on the lower molars: the Pleistocene to recent Eurasian genus, *Camelus*. Webb (1965) suggested that "some large, late Clarendonian species of *Procamelus*, like *P. grandis* or *P. occidentalis* is the most likely North American ancestor to the extant Asian camels" (i.e., *Camelus*). No relationship is suggested between the small Warren camelid and *Camelus*. The small Warren camelid differs from *Procamelus* by lacking P_{2-3} . In *Lama*, the P_2 and P_3 are lost, but the anteroexternal stylids on the lower molars are very strong. In summary, the affinities of this

small Warren camelid are uncertain, however, it appears to be morphologically advanced relative to known Hemphillian forms.

Family ANTILOCAPRIDAE Gray, 1866 cf. Sphenophalos Merriam, 1909

Material: UCMP 29800 – miscellaneous postcranial elements including an astragalus, proximal phalanx, and distal metapodial fragments; UCMP 29801 – two upper premolars.

Locality: UCMP 29800 and 29801 - locality V-2503.

Description and Discussion: Lacking horn cores, it is extremely difficult to identify late Tertiary antilocaprids even at the generic level. An uncertain identification of cf. *Sphenophalos* is made in this case because the Warren material is indistinguishable from *Sphenophalos* specimens from Thousand Creek, Nevada, that were examined in the collections at the Los Angeles County Museum of Natural History.

TABLE 13. Measurements of Camelid gen. et. sp. indet. Dimensions in mm.

Specimen	A.P. Length
UCMP 320110 P ₄ -M ₃	83.2
UCMP 320110 P ₄	13.9
UCMP 320110 M ₁	16.2
UCMP 320110 M ₂	21.5
UCMP 320110 M ₃	31.6
UCMP 320113 M ₂	21.3
UCMP 320115 M ₃	31.8
UCMP 320089 M ¹⁻³	57.0

Biostratigraphy

Nearly all of the fossil mammals from the Horned Toad Formation have been collected within Member Two. The maximum stratigraphic separation of fossil localities from Member Two is approximately 20 m (Figure 62). Analysis of the fossils from below the Lawlor Tuff reveals no observable morphologic variation with stratigraphic position. All of the specimens collected from below the Lawlor Tuff in Member Two are considered to represent a single faunal unit, the Warren Local Fauna. Eighteen of the 24 taxa are represented from a single locality (RV-7702), where W. Daily and colleagues from the University of California, Riverside (UCR) collected, washed, and sorted a large volume of fossiliferous sediment.

May (1981a) and earlier references considered all of the fossils from the Horned Toad Formation as the Warren Local Fauna. Based on the subsequent recognition of the Lawlor Tuff superjacent to most of the fossils in the Warren Local Fauna, with an age close to the Hemphillian/Blancan boundary, it is important to analyze the fossils from above this stratigraphic marker for evolutionary differences. At present, only two taxa are identifiable from localities above the Lawlor Tuff including *Jacobsomys dailyi* and *Dinohippus edensis*. Specimens of these taxa are limited and do not provide evidence for a more advanced stage of evolution than those below the Lawlor Tuff.

Guided by M. Woodburne, B. Reynolds and volunteers from the Mojave River Valley Museum in Barstow, California, collected a large volume of matrix from a locality along the north limb of the Warren syncline in the lower part of Member Four above the Lawlor Tuff. Numerous bone fragments and a limb bone of a small mammal were found during surface prospecting at this locality in 2006, although no identifiable fossils have yet been recovered from the washed matrix.

The majority of fossil mammal localities in Member Two are from sediments exhibiting reversed magnetic polarity (Figure 62). Sites RV-8105 and RV-8120 are shown correlative with the lower part of the overlying normal polarity magnetozone. However, no paleomagnetic samples were collected at these localities, and the lowest definitive normal polarity site is the Lawlor Tuff that occurs stratigraphically above these localities. The suggested correlation of these fossil localities with the lower part of Chron 3n.3n is simply based on the arbitrary placement of the polarity boundary midway between the highest reversed polarity site and the lowest normal polarity site. Taxa from these sites include *Dinohippus edensis* that is also found above the Lawlor Tuff and cf. Agriotherium.

A single locality (RV-8131) was discovered in the lower strata of Member One and may record a fauna distinct from the Warren Local Fauna. This suggestion is based on a single fragment of an upper cheek tooth of a horse that has very complex fossette borders and is unlike the teeth of *Dinohippus edensis*.

Age and Correlation

Twenty-four mammalian taxa have been identified in the Warren Local Fauna. A late Hemphillian age is based on comparison with other faunas and assessment of the stage of evolution of the fossils.

The occurrence of *Cryptotis sp.* in the Warren Local Fauna represents a range extension of this genus. Lindsay et al. (1984) pointed out that shrews are rare in Hemphillian faunas, becoming more common and diverse in the Blancan. Repenning (1967) incorrectly assigned a shrew from the late Hemphillian Christmas Valley Local Fauna of Oregon to Cryptotis adamsi. The oldest irrefutable occurrence of C. adamsi would be from the Blancan Rexroad Fauna of Kansas (Hibbard 1953). Wagner (1981) reported Cryptotis from the late Hemphillian Modesto Reservoir Local Fauna. However, no articular condyle or coronoid process is known from these specimens (Wagner, personal commun., 1980). As discussed in the systematics section, Cryptotis sp. from Warren shows a number of characters that are interpreted as being more primitive than C. adamsi.

The material assigned to cf. *Scapanus* is of no help in determining the age of the fauna. *Scapanus*



FIGURE 62. Summary of the lithostratigraphy, magnetostratigraphy, and biostratigraphy of the Horned Toad Formation. Open squares represent reverse polarity, closed squares represent normal. Vertical bars next to locality labels represent stratigraphic range associated with each locality.

ranges from Clarendonian to Recent faunas in North America.

Hypolagus vetus occurs in both early and late Hemphillian faunas of North America. White (1987) considers *H. vetus* to be restricted to the Hemphillian and Blancan of the western USA and Baja, California.

Hypolagus edensis is known from the late Hemphillian, Redington and Mt. Eden Local Faunas (Arizona and California), as well as from a number of Local Faunas of Blancan age including Hagerman (Idaho) and Taunton (Washington) (White 1987).

The new geomyid *Prothomomys warrenensis* is very advanced relative to most Hemphillian gophers. In development of hypsodonty, *P. warrenensis* approaches the morphology of the Blancan to Recent genus *Thomomys. Prothomomys* provides a potential ancestor for *Thomomys gidleyi*, the oldest record of which is early Blancan (Gustafson 1978). A marked similarity in dP₄ morphology suggests a close relationship of *P. warrenensis* with *Parapliosaccomys oregonensis* Shotwell from the late Hemphillian McKay Reservoir Local Fauna of Oregon.

The small *Perognathus* is most similar to *P. gidleyi* Hibbard from the early Blancan, Rexroad Fauna, but the temporal significance of this comparison is uncertain.

May (1981b) considered the hypsodont cricetine *Repomys gustelyi* to be more primitive than *R. maxumi* that is known from the early Blancan Maxum Local Fauna in California and from early Blancan sediments in the San Timoteo badlands (May and Repenning 1982; Albright 1999). *R. gustelyi* has been identified from a single tooth in the San Timoteo section associated with sediments correlated with late Hemphillian taxa (Albright 1999). Voorhies (1990) includes *R. gustelyi* in faunal lists from both Santee and Devil's Nest Airport Local Faunas in Nebraska, both of which are considered latest Hemphillian. Tedford et al. (2004) list *Repomys* (*R. gustelyi*) as one of the defining taxa for the late late Hemphillian (Hh4).

Postcopemys valensis is known from the Hemphillian of Oregon (Shotwell 1967). The two species of *Peromyscus* are of little value for deter-

mining age although *P*. sp. A is similar to *P. kansasensis* from the Blancan Rexroad Fauna (Hibbard 1941).

Jacobsomys has been previously identified from the early Blancan Verde Valley Local Fauna, Arizona (Czaplewski 1987). J. verdensis is also present in the early Blancan Maxum Local Fauna (Lindsay and Czaplewski 2011). Jacobsomys dailyi represents a range extension of this genus into the late Hemphillian.

The three large carnivores in the Warren Local Fauna are widespread in late Hemphillian faunas of North America. The Borophagus is similar to B. secundus, which has been identified from a large number of faunas from southern and southwestern United States to Honduras. The bear, Agriotherium, is most commonly found in late Hemphillian (Hh3 and Hh4) age faunas in North America (Tedford et al. 2004). Agriotherium is thought to have been replaced by the Eurasian immigrant Ursus in faunas of Blancan age. More recently, Samuels et. al., (2009) report Agriotherium from sediments of Blancan age in Idaho, however the material is fragmentary and taxonomic identity is unclear. The saber toothed cat, Machairodus coloradensis, is known from Wikieup, Coffee Ranch, Wray, Aphelops Draw, and Edson. Machairodus probably immigrated to North America at the same time as Agriotherium (Tedford et al. 2004), but its range extends into the Blancan.

The gomphothere, *Rhynchotherium* sp. cf. *R.* edensis, is very similar to *R.* edensis from the late Hemphillian Mt. Eden Local Fauna (Frick 1933). The shorter enamel bands on the lower tusks suggest that *Rhynchotherium* from Warren may be slightly more advanced than *R.* edensis although the two adult lower tusks are from a single individual and intra-population variability of this character is unknown.

Pliomastodon vexillarius is also present in the Mt. Eden Local Fauna and is known elsewhere from faunas of late Hemphillian to late Blancan age (Madden 1980).

The horse, *Dinohippus edensis*, is known from the late Hemphillian Mt. Eden Local Fauna (Frick 1921; MacFadden 1998).

The *Teleoceras* material from Warren is very similar to *T.* cf. *T. fossiger* reported by Stirton (1939) from the Pinole Tuff Local Fauna of late Hemphillian age. However, *Teleoceras* is a common rhino in North America throughout much of the Miocene (Prothero 1998).

Megatylopus ranges from the late Clarendonian to the early Blancan in the western USA (Honey et al. 1998). Both *Megatylopus* cf. *M. matthewi* and *Hemiauchenia vera* are known from the Coffee Ranch Local Fauna, the San Juan and Rak Camel Quarries of the Chamita Formation and the Wikieup Local Fauna all of which are late Hemphillian faunas. *Hemiauchenia vera* is also known from the Ogallala Group, Nebraska (including Santee and Devil's Nest Airstrip Local Faunas); Ogallala and Ash Hollow Formations, Kansas; Upper Bone Valley Fauna, Florida; Yerington, Nevada; Modesto Reservoir Local Fauna, California, and the Ocote Local Fauna, Mexico (Honey et al. 1998).

The small indeterminate camelid seems to be more derived than other known Hemphillian forms. The lack of P_2 and P_3 parallels the morphology of the Pleistocene to recent genus *Camelus*.

Faunal comparisons suggest a late Hemphillian age for the Warren Local Fauna with close similarities to Mt. Eden, Pinole, Yepomera, and Santee/Devil's Nest Airport Faunas. At the generic level, the Warren and Mt. Eden Faunas share Hypolagus, Repomys, Agriotherium, cf. Prosthennops, Dinohippus, Rhynchotherium, and Pliomastodon. At the specific level they share H. edensis, R. gustelyi, D. edensis, and P. vexillarius. The Warren Local Fauna and Pinole Tuff Local Fauna share Machairodus, Borophagus, Dinohippus, and ?Sphenophalos. The Warren Local Fauna shares Dinohippus, Machairodus, Agriotherium, cf. Prosthennops, and Teleoceras with the Yepomera Local Fauna of Mexico. The Warren Local Fauna shares Hypolagus, Spermophillus, Perognathus, Repomys gustelyi, Borophagus, Agriotherium, Machairodus, Dinohippus, Teleoceras, and Hemiauchenia cf. H. vera, with the Santee/Devil's Nest Airstrip Faunas of Nebraska (Voorhies 1990).

Tedford et al. (2004) showed the Warren Local Fauna correlative with other late late Hemphillian (Hh4) Faunas including the Mt. Eden Local Fauna (California), the Washoe Local Fauna (Nevada), the Etchegoin sites (California), the Pinole Local Fauna (California), the Santee Local Fauna (Nebraska), the Christian Ranch Local Fauna (Texas), the Yepomera Local Fauna (Mexico), the Ocote Local Fauna (Mexico), and the Palmetto Local Fauna of Florida. The Mt. Eden Local Fauna is from reversed polarity sediments interpreted as C3r (5.23 - 5.89 Ma) (Albright 1999), the Washoe Local Fauna is overlain by a tuff dated at 4.96 +/-0.02 (Lindsay et al. 2002), the Etchegoin sites are overlain by the Lawlor Tuff (4.83 +/- 0.04 Ma), the Pinole Local Fauna is associated with the Pinole Tuff dated at 5.2 ± 0.1 Ma (Evernden et al. 1964;

Sarna-Wojcicki 1976), the Santee Local Fauna is overlain by the Santee Ash dated at 5.0 ± 0.2 Ma, the Yepomera Local Fauna is from reversed polarity sediments interpreted as Chron 3n.3r (4.896 – 4.997 Ma) (Lindsay et al. 2002).

Prothomomys warrenensis n. gen. n. sp., Jacobsomys dailyi n. sp., Camelidae gen. et. sp. indet., Peromyscus sp. A, and possibly Rhynchotherium cf. R. edensis, represent morphologically advanced forms relative to known late Hemphillian taxa and are consistent with a late late Hemphillian age for the Warren Local Fauna associated with reversed polarity sediments correlated with Chron 3n.3r and overlain by the Lawlor Tuff dated at 4.83 ± 0.04 Ma. The Lawlor Tuff is the stratigraphically lowest normal polarity site in the sampled polarity sequence in the Horned Toad Formation and the 4.83 ± 0.04 Ma Ar⁴⁰/Ar³⁹ date is consistent with Chron 3n.3n (Sidufjall) (4.799 - 4.896 Ma, Lourens et al. 2004). In addition to many other known occurrences in California and Nevada, the Lawlor Tuff has also been identified at the top of the Etchegoin Formation in the Kettleman Hills, California, just above the Etchegoin Sites fauna of latest Hemphillian age (Hh4, Tedford et al. 2004). The age of the Warren Local Fauna and, by association, Member Two of the Horned Toad Formation is approximately 4.85 - 5.0 Ma. If the Hemphillian-Blancan boundary can be recognized in the Horned Toad Formation, it is likely younger than the Lawlor Tuff (4.83 ± 0.04 Ma).

CONCLUSIONS

The Horned Toad Formation includes five members that record alluvial fan, fluvial, lake margin, and lacustrine deposition within a relatively small basin just south of the active Garlock fault in the late Miocene-early Pliocene. These sediments northwest-southeast contractional experienced deformation during the Pliocene-Pleistocene accommodated by basement involved reverse faults and associated open folds. Paleomagnetic data suggest that the Horned Toad Hills may have experienced significant clockwise rotation since about 4.5 Ma. Member Two of the Horned Toad Formation has yielded 24 taxa of fossil mammals including a new genus of mouse Repomys (previously described), a new genus of gopher, a new species of the mouse Jacobsomys, and probably a new species of the shrew Cryptotis. Analysis of this fauna suggests affinities with other late Hemphillian faunas from California, Nevada, Nebraska, Texas, and Mexico. The Warren Local Fauna contains five taxa of cricetid rodents including both hypsodont and brachydont cricetines and sigmodontines reflecting the apparently rapid diversification of these mammals during the late Miocene to early Pliocene in the southwestern USA. The Lawlor Tuff has been identified in the Horned Toad Formation and overlies most of the fossil mammal localities. This tuff has been dated elsewhere in California at 4.83 ± 0.04 Ma. Magnetostratigraphy from the Horned Toad Formation is correlated with Chrons 3n.3r, 3n.3n, and 3n.2r suggesting an age range of approximately 5.0 - 4.6 Ma. These constraints suggest an age for the late late Hemphillian Warren Local Fauna of 4.85 - 5.0 Ma. Identification of the Hemphillian/Blancan boundary in the Horned Toad Formation will depend on future identification of definitive Blancan taxa above the Lawlor Tuff.

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