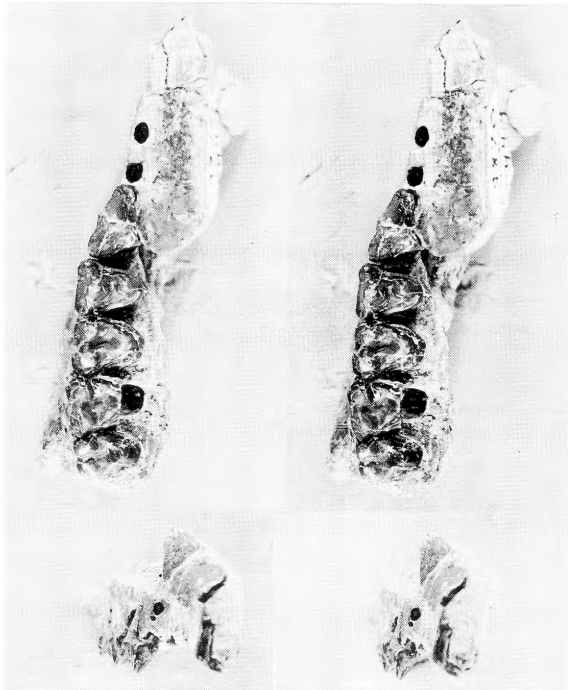


BUNODONT ARTIODACTYLS (MAMMALIA)
FROM THE UINTAN (MIDDLE EOCENE)
OF SAN DIEGO COUNTY, CALIFORNIA

by

Stephen L. Walsh



No. 37

30 September 2000

Proceedings of the

San Diego Society of Natural History



PROCEEDINGS

of the

San Diego Society of Natural History

Founded 1874

Number 37

30 September 2000

Bunodont Artiodactyls (Mammalia) from the Uintan (Middle Eocene) of San Diego County, California

Stephen L. Walsh

Department of Paleontology, San Diego Natural History Museum, P.O. Box 121390, San Diego, California 92112-1390

ABSTRACT.—This report describes new specimens of several bunodont artiodactyl taxa from Uintan (middle Eocene) rocks of San Diego County. *Antiacodon venustus* was previously known only from the upper part of the Bridger Formation but is now recorded from the early Uintan Friars Formation and constitutes another “Bridgerian holdover taxon” present in the latter unit. A single distinctive upper molar proves the occurrence of a second antiacodontine species in the Friars Formation, but more material is needed to identify this taxon. *Tapochoerus egressus* was previously known only from the late Uintan part of the Sespe Formation in Ventura County but is now recorded in San Diego County from the upper part of member C of the Santiago Formation. This occurrence adds to the already high degree of faunal similarity between the San Diego and Ventura County areas during late Uintan time. *Tapochoerus mcmillini* is a relatively small new species of the genus described from late Uintan strata of the Mission Valley Formation and member C of the Santiago Formation. It occurs lower in member C than *T. egressus*. The large helohyine genus *Achaenodon* was previously known only from early Uintan strata of the Rocky Mountain region and is now recorded from the Friars Formation. The available specimens are most similar to *A. robustus*. Two associated helohyine upper molars from the lower tongue of the Friars Formation are assigned to the rare taxon *Parahyus* and may represent a new species of this genus, which was previously known only from the early Uintan(?) of Wyoming and Texas. While the diversity of bunodont artiodactyls in the California Uintan is significantly greater than previously known, this fauna still lacks numerous “homacodon” taxa that are common in Uintan rocks of the western interior.

INTRODUCTION

Eocene artiodactyls from southern California were first described from the Sespe Formation in Ventura County. Stock (1934a) named the supposed hyopsodontid “condylarth” *Hyopsodus egressus* from the late Uintan Tapo Canyon local fauna. Stock (1934b) also named the hypertragulid genus *Simimeryx* from the Duchesnean Pearson Ranch local fauna of the Sespe. Finally, Stock (1936) named the new subgenus and species *Leptoreodon (Hesperomeryx) edwardsi* from the Tapo Canyon local fauna. In his review of the “upper” (now regarded as middle) Eocene artiodactyls of North America, Gazin (1955) concurred with Stock’s analysis of *Simimeryx* and *Leptoreodon (Hesperomeryx) edwardsi*. However, McKenna (1959) recognized that Stock’s species *Hyopsodus egressus* actually pertained to a new genus of “dichobunid” artiodactyl, which he named *Tapochoerus*.

Golz (1976) reviewed the Eocene selenodont artiodactyls of southern California. He named the basal oromerycid genus *Merycobunodon* from the early Uintan Friars Formation and named several new species of *Protoreodon*, *Protylopus*, and *Leptoreodon* from Uintan and Duchesnean strata of San Diego and Ventura counties. In addition, Golz named the new camelid species *Poebrodon californicus* from the latest Uintan and/or Duchesnean Laguna Riviera local fauna of San Diego County and recognized the advanced oromerycid *Eotylopus* from the Duchesnean of Ventura County. Kelly (1990), Kelly et al. (1991), and Kelly and Whistler (1994) have updated the occurrences of various artiodactyl taxa from the Sespe Formation. The most recent contribution to our knowledge of the Eocene artiodactyls of southern California is that of Theodor (1999), who named

a new species of *Protoreodon* from the late Uintan of San Diego County.

Golz (1976:17, 27) noted the rarity of bunodont artiodactyls (“dichobunids”) in existing California collections but suggested that “more dichobunids may be added to the Eocene fossil record of California as collecting continues in Uinta B equivalents in San Diego, and perhaps animals related to *Tapochoerus egressus* will be discovered.” During the past sixteen years, PaleoServices, Inc., and the San Diego Natural History Museum have conducted extensive paleontological monitoring of construction-related grading operations in San Diego County. These salvage efforts have yielded important new collections of Eocene mammals; among them are several taxa of bunodont artiodactyls. A few specimens of bunodont artiodactyls have also been located in the San Diego Eocene collections of the Natural History Museum of Los Angeles County and the University of California Museum of Paleontology, Berkeley. This report describes the new material and reviews the paleobiogeographic distribution of middle Eocene bunodont and bunoselenodont artiodactyl taxa in southern California and the western interior.

Golz and Lillegraven (1977), Walsh (1996), and Walsh et al. (1996) discussed various Eocene local faunas and geographic collecting districts of San Diego County. Walsh et al. (1996) provided a reinterpretation of the Friars Formation and Poway Group (Kennedy and Moore, 1971; Kennedy, 1975; Kennedy and Peterson, 1975) that is critical to understanding the stratigraphic provenance of the Uintan mammals of southwestern San Diego County. Briefly, the Friars Formation is subdivided informally into three parts: a lower sandstone and mudstone tongue, a middle conglomerate tongue, and an upper

sandstone and mudstone tongue, all of which appear to be entirely of early Uintan age. West of the western pinchout of the conglomerate tongue, the lower and upper tongues of the Friars cannot be distinguished; these sandstone-dominated strata are referred to as the Friars Formation, undifferentiated.

CLASSIFICATION

Gazin's (1955) traditional classification of North American Eocene "dichobunid" artiodactyls has been modified by the rather different arrangements of Gentry and Hooker (1988), McKenna and Bell (1997), and Stucky (1998). Gentry and Hooker's (1988) analysis placed *Antiacodon* and leptocoerines within the Selenodontia, and helohyines within the Bunodontia. Gentry and Hooker (1988) regarded Selenodontia and Bunodontia as unranked taxa between order and suborder, named the new selenodont suborder Merycotheria to include Ruminantia and various "dichobunids" (excluding the "Uintan homacodontines"), and named the new family Bunomerycidae to include the Uintan "homacodontines" *Bunomeryx*, *Hylomeryx*, *Mesomeryx*, *Mytonomeryx*, and *Pentacemylus*. Gentry and Hooker (1988) assigned the Bunomerycidae to the suborder Tylopoda within Selenodontia, and apparently regarded leptocoerines and *Diacodexis metsiacus* as *incertae sedis* within Selenodontia.

McKenna and Bell (1997) recognized Suiformes, Tylopoda, and Ruminantia as three suborders of Artiodactyla. They retained Diacodexinae, Leptochoerinae, Homacodontinae, and the European Dichobuninae as subfamily-level taxa within the Dichobunidae; they raised the Helohyinae to family rank and included the Asian genera *Gobiohyus* and *Pakkokuhys* within it. McKenna and Bell also placed the Dichobunidae, Helohyidae, Cebochoeridae, and Mixtotheriidae within the superfamily Dichobunoidea and assigned the Dichobunoidea to the suborder Suiformes (= Bunodontia).

Stucky (1998) did not recognize the superfamily Dichobunoidea. He restricted the family name Dichobunidae to European taxa and assigned various former North American "dichobunids" to "*Diacodexis*," the "homacodonts," and the subfamilies Antiacodontinae, Leptochoerinae, and Helohyinae. Stucky left the Antiacodontinae and Leptochoerinae *incertae sedis* within Artiodactyla and regarded the "homacodonts" and the Helohyinae (excluding *Gobiohyus* and *Pakkokuhys*) as basal members of the suborder Selenodontia.

Obviously, the cladistic relationships of many of these early artiodactyls are unclear, and Stucky's (1998) conservative approach has merit in that it calls attention to the magnitude of our ignorance. Bunodont taxa described here pertain only to the Antiacodontinae and Helohyinae as envisioned by Stucky (1998). Specimens of the leptocoerine *Ibarus* sp. cf. *I. ignotus* recorded by Walsh (1996: table 2) will be described elsewhere.

METHODS

Specimens are sometimes introduced in the form "XXXX/YYYY," where "XXXX" represents the locality (Loc.) number and "YYYY" the specimen number. Unless stated otherwise immediately below, measuring orientations and measuring endpoints of cheek teeth follow those of Golz (1976:3). For upper molars, the anteroposterior (AP) axis passed through the apices of the paracone and metacone. The anterior and posterior width was measured perpendicular to the AP axis, from the lingual base of the protocone to the labial base of the paracone and metacone, respectively. For lower molars, the trigonid width and talonid width were oriented perpendicular to the AP axis and respectively measured the maximum transverse width of the anterior and posterior halves of the tooth. Depending on the size of the specimen, measurements of teeth were made either with an Ehrenreich Photo-Optical Industries "Shopscope" to the nearest 0.01 mm, or with a pair of vernier calipers to the nearest 0.1 mm. Abbreviations are as follows:

Dental:

- AP, anteroposterior length of upper and lower teeth.
 AW, anterior width of upper molars.
 C and c, upper and lower canine, respectively.
 DP and dp, upper and lower deciduous premolar, respectively.
 i, lower incisor.
 L and R, left and right, respectively.
 P and M, upper premolar and molar, respectively.
 p and m, lower premolar and molar, respectively.
 PW, posterior width of upper molars.
 W, maximum transverse width (for upper and lower premolars).
 WTRI, maximum width of trigonid.
 WTAL, maximum width of talonid.
 Institutional:
 AMNH, American Museum of Natural History, New York.
 BCHS, Bouxwiller collection of the Muséum d'Histoire Naturelle, Basel, Switzerland.
 CM, Carnegie Museum of Natural History, Pittsburgh.
 DMNH, Denver Museum of Natural History.
 LACM (CIT), original collections of the California Institute of Technology, now housed at the Natural History Museum of Los Angeles County, Los Angeles.
 MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.
 MPM, Milwaukee Public Museum.
 SDSM, South Dakota School of Mines and Technology, Rapid City.
 SDSNH, San Diego Natural History Museum.
 SMNH, Royal Saskatchewan Museum, Regina.
 TMM, Texas Memorial Museum, University of Texas at Austin.
 UCM, University of Colorado Museum of Geology, Boulder.
 UCMP, University of California Museum of Paleontology, Berkeley.
 UM, University of Michigan Museum of Paleontology, Ann Arbor.
 USNM, United States National Museum, Washington, D.C.
 UW, University of Wyoming, Laramie.
 YPM, Yale Peabody Museum, New Haven.
 YPM-PU, original Princeton University collections, now owned by YPM.

SYSTEMATIC PALEONTOLOGY

Order Artiodactyla Owen, 1848

Suborder *incertae sedis*

Family *incertae sedis*

Subfamily Antiacodontinae Gazin, 1958

Remarks.—McKenna and Bell (1997:401) placed *Antiacodon* and *Auxontodon* in the subfamily Homacodontinae, but I follow Storer (1984a) and Stucky (1998) in uniting these two genera with *Tapochoeris* and *Neodiocodexis* in the subfamily Antiacodontinae. McKenna and Bell (1997) also assigned *Antiacodon* to the superfamily Dichobunoidea and the latter to the suborder Suiformes. This conflicts with Gentry and Hooker's (1988, fig. 9.8) placement of *Antiacodon* within the suborder Selenodontia. Stucky's (1998) conservative approach is partly followed here by leaving the familial and subordinal assignment of the Antiacodontinae in doubt.

Stucky (1998) characterized the Antiacodontinae by their possession of (1) a strong cristid obliqua that extends to the metaconid apex, (2) a paraconid subequal in size to or larger than the metaconid on m1-3, (3) a small cingular hypocone, and (4) a weak accessory cusp (anterocone) on the anterior cingulum. Characters 1, 2, and 4 are potential autapomorphies for the taxon, although in *Tapochoeris* the anterocone is absent or very weak and the paraconid is partially or completely merged with the metaconid on m2-3. Upper molars of all antiacodontine genera have a distinct gap between the protocone and

metaconule (one new species of *Tapochoerus* excepted), but this character is probably primitive for the subfamily, because it also occurs in *Hexacodus*, *Homacodon*, and *Microsus* (although not in *Diacodexis*).

Antiacodon Marsh, 1872

Type Species.—*Antiacodon venustus* Marsh, 1872.

Included Species.—*Antiacodon pygmaeus* (Cope, 1872), *A. furcatus* (Cope, 1873a), and *A. vanvaleni* Guthrie, 1971.

Diagnosis.—Differs from *Auxotodon* in having upper molars that are lower-crowned, with weaker mesostyles, conules, cingula, and hypocones, and in having a ventral border of the dentary that is slightly rather than strongly convex. Differs from *Neodiacyodexis* in lacking crenulated enamel, lacking a cuspule on the posterior cingulum of P4, and in having upper molars with weaker lingual cingula and less crescentic cusps and conules. Differs from *Tapochoerus* in having upper molars with (weak) mesostyles, stronger anterocones, and stronger labial cingula, and in having a (weak) metaconid on p3, large separate paraconids on m1–3, and less anteroposteriorly elongated lower molars. No autapomorphies known.

Known Distribution.—Late Wasatchian to late Bridgerian (late early Eocene to early middle Eocene) of the Rocky Mountain region (Willwood, Wasatch, Wind River, Green River, Bridger, Huerfano,

and Aycross formations; Stucky, 1998); early Uintan (early middle Eocene) of southern California (Friars Formation).

Antiacodon venustus Marsh, 1872

Figures 1–3

Diagnosis.—Largest known species of the genus; linear dimensions of cheek teeth ranging from 15% to 43% larger than in *Antiacodon pygmaeus*, *A. furcatus*, and *A. vanvaleni*. Differs from *A. furcatus* in having a relatively weaker postcingulid and a relatively weaker hypoconulid that is more closely appressed to the entoconid on m1–2. Differs from *A. vanvaleni* in having stronger paraconids. No morphological autapomorphies known.

Referred Specimens.—Friars Formation, undifferentiated: SDSNH 3784/49223, LM2?; 3784/49550, LM2?; 3784/51379, Ldp4?; 3784/49170, L dentary fragment with p4–m3; 3784/50565, L dentary fragment with p4–m3 + alveoli for p2–3; 3784/50576, Lm3; LACM (CIT) 249-S/56127, Lm3. UCMF V-68101/104316, LM3.

Upper tongue of Friars Formation: SDSNH 3611/45300, RM2. Conglomerate tongue of Friars Formation: SDSNH 3621/55891, L dentary fragment with p4 + m2–3. SDSNH 3824/60871–60872, associated RM1 and RM2, respectively.

Description.—No skull, maxillary material, or upper teeth ante-

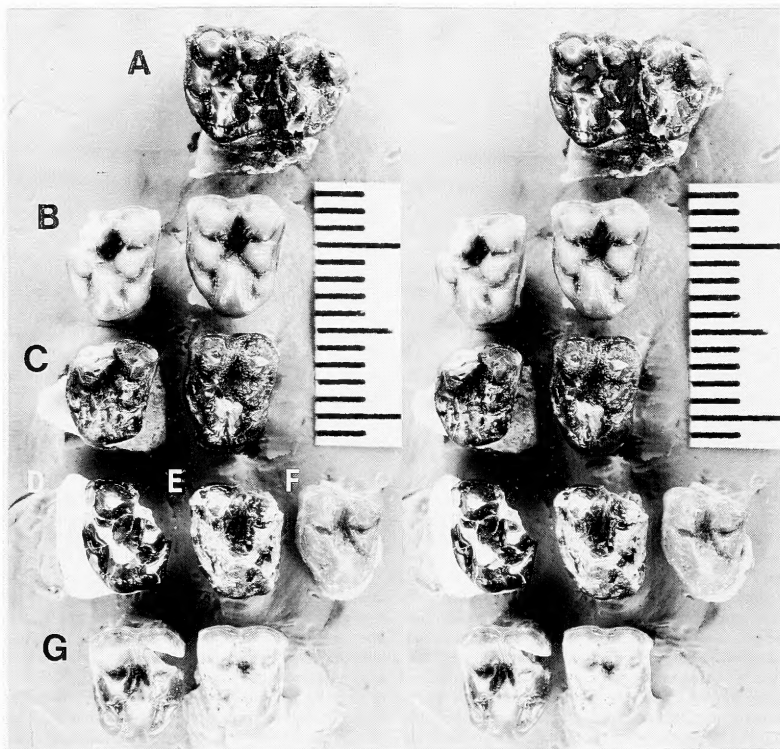


Figure 1. Stereophotographs in occlusal view of upper molars of *Antiacodon venustus* from the Bridger and Friars Formations: (A), YPM 37189, L maxillary fragment with M2–3; (B), UCM 57498 and 57499, associated LM1 and LM2, respectively; (C), MPM 6717, associated LM1–2; (D), SDSNH 49550, LM2?; (E), SDSNH 49223, LM2?; (F), UCMF 104316, LM3; (G), SDSNH 60872 and 60871, associated RM2 and RM1, respectively. Scale divisions in mm.

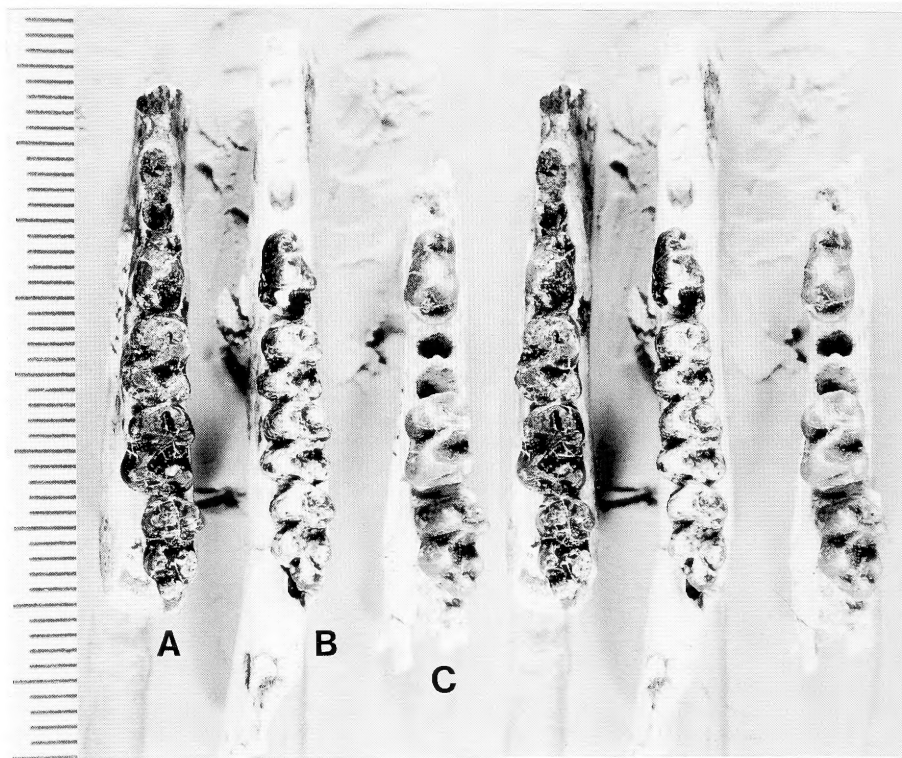


Figure 2. Stereophotographs in occlusal view of lower dentitions of *Antiacodon venustus* from the Friars Formation: (A), SDSNH 49170, L dentary fragment with broken roots of p3 + p4-m3; (B), SDSNH 50565, L dentary fragment with alveoli for p2-3 + p4-m3; (C), SDSNH 55891, L dentary fragment with p4 + m2-3. Scale divisions in mm.

rior to the molars are known. Five isolated upper molars are available from the Friars Formation (Figures 1D-G). SDSNH 60871 and 60872 (Figure 1G) almost certainly pertain to the same individual and can be confidently identified as M1 and M2, respectively. As expected from maxillary specimens of *Antiacodon pygmaeus* with M1-2 in place, the M2 is slightly larger than M1. The paracone and metacone of M1-2 are conical and subequal in height and diameter. The weak postparacrista and premetacrista barely converge but do not form a distinct centrocrista. A strong ectocingulum is present along the entire preserved labial border of each tooth and bears a very weak mesostyle. Distinct, subequal paraconules and metaconules are present, with weak preparaconular and postmetaconular wings. The protocone is conical, and shorter but broader than the labial cusps. There is a distinct gap between the protocone and the metaconule. A strong anterior cingulum extends from the anterolingual base of the protocone all the way to the weak parastyle. A weak cusplule (anterocone) is present on the anterior cingulum below the protocone on all four M1-2s. The hypocone is distinct but much smaller than the protocone and located at the posterolingual base of the latter. A posterior cingulum extends from the hypocone apex to the metastyle area. SDSNH 49550 and 49223 (Figures 1D-E) have a relatively blunt lingual margin, are slightly larger than SDSNH 60871 (undoubted M1), and are tentatively identified as M2s. M1-2 are

three-rooted. The lingual root is the largest and is essentially cylindrical, while the two smaller labial roots are subequal in diameter and slightly compressed anteroposteriorly.

A single M3 is known (UCMP 104316, Figure 1F). The tooth is essentially complete, lightly worn, and pentagonal in occlusal outline. The presence of a distinct anterior appression facet and the absence of a posterior facet confirm the tooth to be an M3. The lingual root is the largest and is essentially cylindrical. The two smaller labial roots are broken away but were subequal in diameter. The paracone is essentially conical and is larger and taller than the conical metacone. A weak rib extends down the anterior face of the paracone to connect with a very weak parastyle. There is no metastyle. The strong labial cingulum is damaged but was clearly complete around the labial border of the tooth. A shallow ectoflexus seems to have been present. The centrocrista is positioned relatively labially and connects the bases of the paracone and metacone. A distinct mesostyle is absent, but this cusplule may have been located on the damaged labial cingulum. The paraconule and metaconule are relatively large. A strong preparaconular wing is present, but a postparaconular wing is absent. The metaconule bears both pre- and postmetaconular wings. The protocone is low and broad, weakly connected to the paraconule, and separated from the metaconule by a distinct gap. The anterior and posterior cingula are quite strong, and

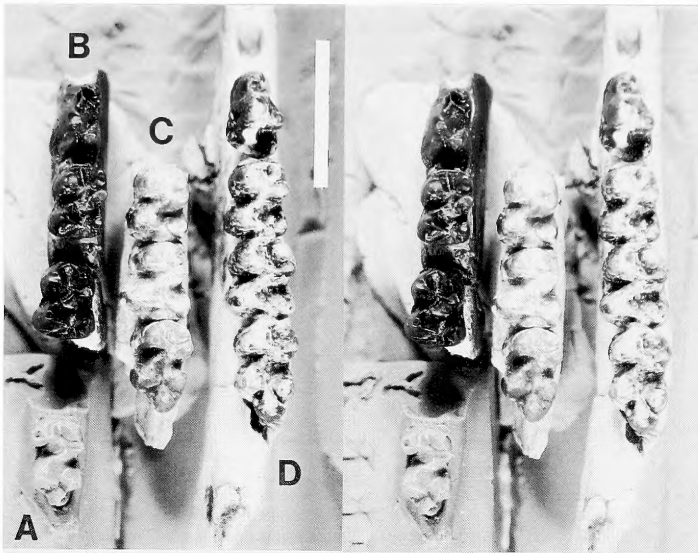


Figure 3. Stereophotographs in occlusal view of lower dentitions of *Antiacodon venustus* from the Bridger and Friars formations: (A), Cast of YPM 11765, Lm3, holotype of *A. venustus*; (B), YPM 13272, L dentary fragment with p4-m2; (C), YPM 16861, L dentary fragment with m1-3; (D), SDSNH 50565, L dentary fragment with alveoli for p2-3 + p4-m3. Scale bar = 10 mm.

almost continuous around the lingual base of the protocone. There is no hypocone and no anterocone.

Three dentary fragments are known, of which SDSNH 50565 is the most nearly complete (Figure 2B). The condyle and coronoid process are not preserved. The depth of the ramus below m1-3 is a nearly constant 9.5 mm and decreases to about 7.0 mm below p3. The ventral border of the dentary is slightly convex as in *Antiacodon* (see Burke, 1969; West, 1984, fig. 7) and not strongly convex as in *Auxontodon pattersoni* (see Gazin, 1958). The masseteric fossa displays a weak ventral division and a deeper dorsal division. The fossa extends anteriorly to a point below about 2.5 mm posterior to the posterior end of m3. The ascending ramus starts to rise from the dorsal border of the dentary immediately posterior to the posterior end of m3. A single tiny mental foramen is present below the anterior root of p3 on SDSNH 49170 but occurs below the posterior root of p3 on SDSNH 50565 and below the anterior root of p4 in SDSNH 55891. As seen in SDSNH 50565, there is a short diastema of about 1.8 mm between p2 and p3.

No lower teeth anterior to p4 are known. The broken roots and/or alveoli for p3 are present in SDSNH 49170 and 50565 and show that this tooth was subequal in size to p4. A possible dp4 is tentatively assigned to *Antiacodon venustus* (SDSNH 51379, not figured). This tooth is unlikely to be a p3, because the p3 in *Antiacodon pygmaeus* is relatively short anteroposteriorly, with a simple trencant crown and very weak metaconid (e.g., MPM 6721; West, 1984, fig. 6). The crown of SDSNH 51379 is heavily worn, but there was clearly a distinct metaconid, paralophid, and paraconid. However, there is no distinctly expanded anterior lobe as in the dp4 of other small artiodactyl taxa in the Friars Formation, such as *Leptoreodon* and cf. *Protylopus*. The talonid appears to have had a distinct hypoconid, a weaker entoconid, and a distinct cristid obliqua. The tooth is anteroposteriorly elongate, with subequal talonid and trigonid widths.

The anterior and posterior roots have been broken away, and their thin-walled remnants are filled with matrix. The AP length of SDSNH 51379 is 6.25 mm (minimum value owing to slight damage), and the maximum width is 3.29 mm.

Three p4s are known, all of which occur in dentary fragments. The protoconid is tall and conical. A distinct metaconid is present on the posterolingual flank of the protoconid on SDSNH 50565 and 55891 (Figures 2B-C) but is very weak on 49170 (Figure 2A). A distinct paraconid is present on 49170 and 50565. Two "paraconids" are present on SDSNH 55891, occurring atop the anterior and posterior ends of the paralophid. A posterolabial cingulid is strong in all three available p4s, while the anterolabial cingulid is weak in SDSNH 49170 and 50565 and absent in SDSNH 55891. The talonid lacks accessory cusplids. A weak cristid obliqua is present on all three p4s, extending from the hypoconulid area up the posterior face of the protoconid.

Two mls are known, both of which occur in dentary fragments (Figures 2A-B). The trigonid is distinctly narrower than the talonid. The strong, conical paraconid is taller than the metaconid and protoconid. A weak anteriorly convex paralophid connects the anterior faces of the paraconid and protoconid. An even weaker metalophid connects the metaconid with the lingual face of the protoconid. A distinct anterior cingulid is present. The strong cristid obliqua extends from the hypoconid apex up the labial face of the metaconid. A weak ectostylid is present in the hypoflexid. The entoconid is conical and much smaller than the hypoconid. A weak hypoconulid is present at the lingual end of the distinct postcingulid and is separated from the entoconid by a narrow notch.

Four m2s are known, three of which occur in dentaries (Figure 2). They are very similar in morphology to the mls, including the invariable presence of a strong paraconid that is well separated from the metaconid. The m2s do differ from the mls in being slightly larger, in

TABLE 1. Measurements (in mm) of cheek teeth of *Antiacodon venustus* from the Friars Formation. Asterisks indicate minimum value because of slight damage, enamel dissolution, or interdental wear.

	P4		M1			M2			M3		
	W	L	AP	AW	PW	AP	AW	PW	AP	AW	PW
SDSNH 49550	—	—	—	—	—	—	6.46	—	—	—	—
SDSNH 49223	—	—	—	—	—	—	6.73	—	—	—	—
SDSNH 60871	—	—	5.13*	5.81	5.94	—	—	—	—	—	—
SDSNH 60872	—	—	—	—	—	5.41	6.72	6.71	—	—	—
UCMP 104316	—	—	—	—	—	—	—	—	4.92	5.95	5.62*
Mean:	—	—	—	—	—	—	6.64	—	—	—	—

	p4		m1			m2			m3		
	AP	W	AP	WTRI	WTAL	AP	WTRI	WTAL	AP	WTRI	WTAL
SDSNH 49170	5.22	3.32	5.88	3.77	4.36*	6.04	4.07*	4.59	6.80*	3.95	3.56
SDSNH 50565	5.86	3.50	5.50	3.80	4.12	5.66	4.15	4.62	6.86	3.97	3.83
SDSNH 55891	6.34	3.61	—	—	—	5.93	4.27	4.55	6.85	4.32	4.11
SDSNH 45300	—	—	—	—	—	5.77	4.16	4.45	—	—	—
SDSNH 50576	—	—	—	—	—	—	—	—	6.47	3.84	3.82
LACM 56127	—	—	—	—	—	—	—	—	6.30	3.56	3.36
Mean:	5.81	3.48	5.69	3.79	4.24	5.85	4.16	4.55	6.66	3.93	3.74

having trigonid widths that are more equal to the talonid widths, and in having weaker or absent ectostylids.

Five m3s are known, three of which occur in dentaries (Figure 2). The trigonid morphology is very similar to that seen in m1–2, including the invariable presence of a strong paraconid that is well separated from the metaconid. However, the m3 entoconid is subequal in size to the hypoconid, and a strong hypoconulid is present on the hypoconulid lobe. A short posterolabial cingulid is present between the hypoconid and hypoconulid. An anterolabial cingulid is complete around the base of the protoconid in SDSNH 50576 but is absent on SDSNH 49170, 50565, 55891, and LACM 56127. All m3s lack an ectostylid. A distinct ridge connecting the hypoconulid with the region between the entoconid and hypoconid is present in SDSNH 50565 but is absent in all other San Diego m3s. Finally, LACM 56127 differs from the other m3s in the sample in having a very weak entoconid. Table 1 provides dental measurements of *Antiacodon venustus* from the Friars Formation; Figure 4 shows bivariate plots for p4–m3.

Comparisons.—Stucky (1998) included several genera in the Antiacodontinae, which are compared to the Friars Formation specimens as follows. The upper molars of *Antiacodon venustus* from the Friars Formation differ from those of the only known specimen of the late Bridgerian species *Neodiadocodex emryi* in that M1–2 of the latter range from 2% to 18% larger in linear dimensions, have strongly crenulated enamel, slightly stronger parastyles, stronger doubled anterocones, larger paraconules and metaconules, stronger pre- and postparaconular and metaconular wings, sharper centrocrisatæ (giving the paracone and metacone a transversely compressed appearance), and a deeper ectoflexus (West and Atkins, 1970).

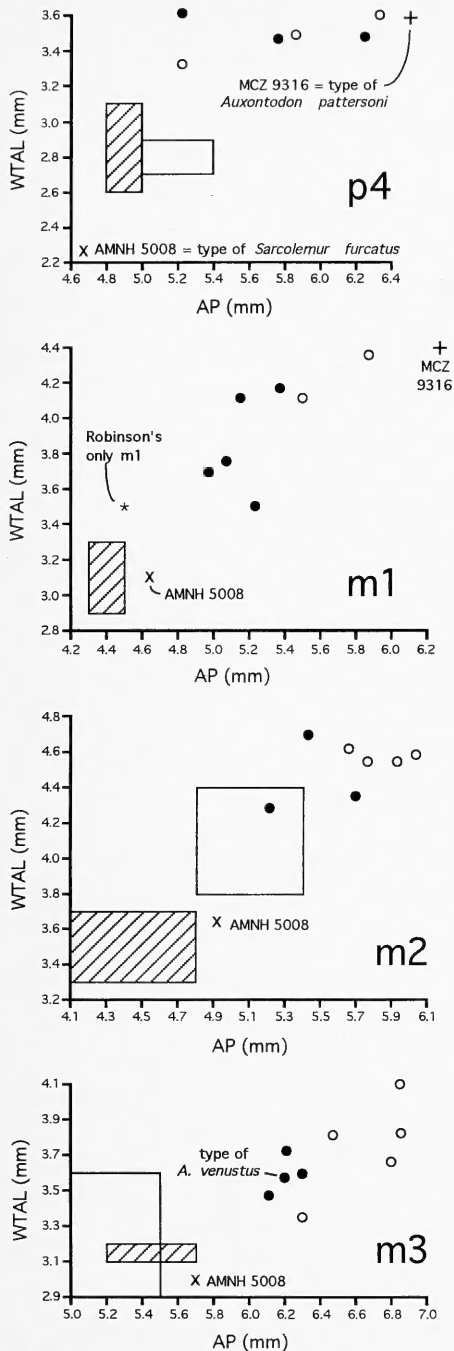
The lower cheek teeth of *Antiacodon venustus* from the Friars Formation differ from those of the late Uintan species *Auxontodon pattersoni* Gazin, 1958, in that the type specimen of the latter (MCZ 9316, Figure 5) has slightly larger and more anteroposteriorly elongated p4–m1, has a tiny but distinct “entoconid” on p4, lacks an ectostylid on m1, has a much deeper dentary whose ventral margin is strongly concave rather than slightly concave, and lacks a short diastema between p2 and p3. However, the p4 in MCZ 9316 is otherwise similar in size, occlusal outline, and paraconid and metaconid development to the p4s in SDSNH 50565 and 55891. The upper molars of *Antiacodon venustus* from the Friars Formation differ from those of the late Uintan species *Auxontodon processus* in that the best-preserved upper molar of the latter species (SMNH P1654.449; M1 or 2) has a much stronger mesostyle, a more strongly ribbed

paracone and metacone, larger conules, a larger hypocone with a ridge connection to the protocone, and a nearly complete lingual cingulum (Storer, 1984a, fig. 8D). The holotype m3 of *Auxontodon processus* (P1654.457) differs from the Friars Formation m3s in having a much larger paraconid than metaconid and in having a much wider trigonid than talonid. Molars of *Auxontodon processus* also range from 17% to 52% larger in linear dimensions than those of *Antiacodon venustus* from the Friars Formation.

The Friars Formation specimens of *Antiacodon venustus* differ from those of the late Uintan species *Tapochoerus egressus* in that the latter has cheek teeth ranging from 12% to 60% larger in linear dimensions, upper molars that lack mesostyles and have a deeper ectoflexus, a weaker paraconid and metaconid on p4, a weaker paraconid on m2, a paraconid merged completely with the metaconid on m3, a shorter hypoconulid lobe on m3, and more anteroposteriorly elongated lower molars (see Stock, 1934a; McKenna, 1959).

The early Bridgerian species *Sarcolemur furcatus* was originally designated as *Antiacodon furcatus* by Cope (1873a), and later transferred to the new genus *Sarcolemur* by Cope (1875). Subsequently, this species has often been regarded as a junior synonym of *Antiacodon pygmaeus* (Cope, 1872). See for example Cope (1884:233), Gazin (1955:23), and McKenna and Bell (1997). In contrast, Guthrie (1971) and Stucky (1998) retained *Sarcolemur* as a distinct genus, with *S. furcatus* the only known species (but note that Guthrie, unlike Stucky, regarded *Hexacodus* Gazin as a junior synonym of *Sarcolemur*). The lower cheek teeth of *Antiacodon venustus* from the Friars Formation differ from those in the type specimen of *S. furcatus* (AMNH 5008; dentary fragment with p4–m3) in that the latter range from 11% to 36% smaller in linear dimensions, are more transversely compressed, have a more transversely compressed protoconid on p4, and have m1–2 with relatively smaller paraconids, stronger postcingulids, and relatively taller hypoconulids that are better separated from the entoconid.

One of the diagnostic characters of *Sarcolemur* cited by Stucky (1998) is the presence of the hypoconulid on the postcingulid in m1–2 (cf. Guthrie, 1971:86). I am dubious about the significance of this character, however, because this location of the hypoconulid is common to all specimens of *Antiacodon* that I have seen, e.g., MPM 5896, YPM 13275, YPM 16865 (*A. pygmaeus*), and YPM 13272, 13273, 16861, and 37188 (*A. venustus*). Nevertheless, the postcingulid is broader and the hypoconulid is better separated from the entoconid in AMNH 5008 than in these specimens. Stucky (1998)



Key to Figure 4

- = *Antiacodon venustus*, Friars Fm.
- = *A. venustus*, Bridger Fm.
- ▨ = rectangle containing West's (1984) measurements of *A. pygmaeus*
- = rectangle containing Robinson's (1966) measurements of *A. p. huerfanensis*

also cited the presence of a strong crest between the hypoconid and entoconid as a characteristic feature of *S. furcatus* (see also Guthrie, 1971:86), but, in my opinion, based on an excellent cast of AMNH 5008, this crest is actually quite weak; its strength is exaggerated in Osborn's (1902, fig. 16) illustration of the type. An additional character that may separate *S. furcatus* from *A. pygmaeus* is the very narrow p4 talonid (2.27 mm) in AMNH 5008, compared to the relatively wide talonid in most p4s of *A. pygmaeus*, e.g., CM 10930 (Burke, 1969), MPM 6721 (West, 1984, fig. 6), and YPM 16865. However, a relatively narrow p4 is present in USNM 417343 (assigned to *A. pygmaeus* by Emry, 1990:207) and UM 100572 and 100759 (assigned to *A. sp.*, cf. *A. pygmaeus* by Gunnell, 1998:125). I again question the generic separation of *Sarcolemur* from *Antiacodon* but retain *A. furcatus* as a distinct species on the basis of its narrow p4 and its strong postcingulid and isolated hypoconulid on m1-2. Note that the p4 in AMNH 5008 is unworn, while the molars are very lightly worn. Thus, dp4 was apparently shed quite early in the lives of individuals of *A. furcatus*; this may cast doubt on my above identification of the well-worn SDSNH 51379 as a dp4 of *Antiacodon venustus*.

The Friars Formation specimens described above are assigned to the genus *Antiacodon* on the basis of their nearly horizontal ventral border of the dentary, their strong well-separated paraconids and metaconids on m1-3, strong cristids obliqua that contact the metaconid, weak mesostyles, lack of crenulated enamel, and relatively small size. The Friars Formation teeth differ from those of *Antiacodon pygmaeus* in ranging from 4% to 31% larger in linear dimensions (based on measurements of West, 1984, Table 2) and in having a relatively narrower p4 talonid. The Friars Formation specimens have only a single mental foramen (although the location of this foramen varies from below the anterior root of p3 to below the anterior root of p4). In contrast, an additional anterior mental foramen was reported below the p2 of *A. pygmaeus* by West (1984:14). Two mental foramina are also present below the p3-p4 contact and below the posterior root of p3 on another dentary of *A. pygmaeus* (YPM 16865).

The Friars Formation teeth are virtually identical in size and morphology to those of the late Bridgerian species *Antiacodon venustus* Marsh, 1872, ranging from about 0% to 15% larger in linear dimensions, based on specimens in the original YPM hypodigm of this species (Table 2). To my knowledge, no specimens of *A. venustus* have ever been figured (including the type; e.g., Gazin, 1952:76). Gazin (1955:23) believed that *A. venustus* and *A. pygmaeus* were synonyms, but Gazin (1976:12) apparently changed his mind when

Figure 4. Bivariate plots of anteroposterior length vs. talonid width of lower cheek teeth of various samples of *Antiacodon* from the Bridger and Friars formations. Note that specimens of *A. venustus* from the Friars Formation tend to be slightly larger than those from the Bridger Formation, but that all teeth of *A. venustus* are well separated from West's (1984) sample of *A. pygmaeus* and are generally well separated from Robinson's (1966) sample of *A. p. huerfanensis*.

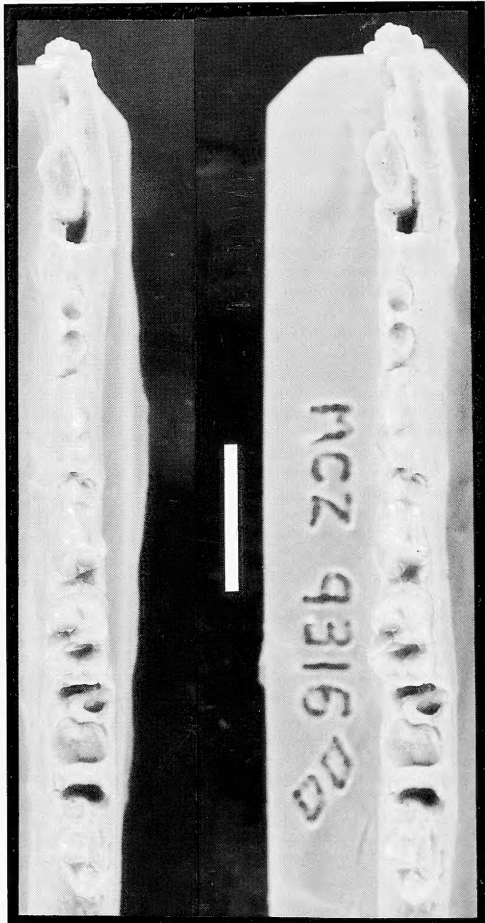


Figure 5. Stereophotograph in occlusal view of cast of MCZ 9316, holotype L dentary of *Aucoctodon pattersoni*, from the Myton Member of the Uinta Formation. Dentary contains broken roots of i1–p2, complete p3–m1, and partial m3. Scale bar = 10 mm.

he noted that two referred specimens of *A. venustus* were present at USNM (see Table 2). I agree with West (1984) and Stucky (1998) that *A. venustus* is a valid species, distinctly larger than *A. pygmaeus*.

The type specimen of *A. venustus* is YPM 11765, a dentary fragment with slightly damaged m3 from the upper part of the Bridger Formation (Marsh, 1872:210–211). This tooth (a cast of which is illustrated in Figure 3A) is slightly smaller than the Friars Formation m3s but is otherwise very similar in morphology. It has a weak connecting ridge between the hypoconulid and the entoconid–hypoconid area, which is a variable character in the Friars sample. Several other YPM and USNM lower dentitions of *A. venustus* are very similar in size and morphology to the Friars Formation teeth, e.g., YPM 13271 (dentary fragment with damaged p4–m3), YPM 13272 (dentary fragment with

p4–m2; Figure 3B), YPM 13273 (dentary fragment with m1), 13277 (dentary fragment with m2 talonid + m3), 16861 (dentary fragment with m1–3; Figure 3C), and USNM 13446 (dentary fragment with m1) and USNM 364903 (dentary fragment with m3 and associated? p3). YPM 13271 and 13272 also have a single mental foramen below the posterior alveolus of p3, as in SDSNH 49170 and 50565. These YPM and USNM specimens of *A. venustus* from the upper part of the Bridger Formation cannot be separated at the species level from the Friars Formation specimens. Figure 4 shows bivariate plots of selected measurements of the lower cheek teeth of *A. venustus* from the Friars and Bridger formations, along with two samples of *A. pygmaeus* measured by Robinson (1966) and West (1984).

Upper dentitions of *Antiacodon venustus* are poorly known. West (1984:44) listed YPM 16861 (includes an isolated P4), YPM 37189 (maxillary fragment with M2–3; erroneously listed by him as YPM 13189), and MPM 6717 (associated M1–2), all from the upper part of the Bridger Formation (Bridger C and D undifferentiated). An associated M1–2 (UCM 57498 and 57499, respectively) was also collected in 1994 from Bridger D by UCM personnel and identified as *A. venustus* by R. K. Stucky.

The M2 in YPM 37189 (Figure 1A) differs from the undoubted M2 from the Friars Formation (SDSNH 60872; Figure 1G) in having a slightly stronger mesostyle and a slightly larger anterocone but is otherwise very similar in size and morphology. UCM 57498 and 57499 (Figure 1B) differ from the Friars Formation M1–2s in having slightly larger conules, slightly larger anterocones, slightly deeper ectoflexi, slightly stronger mesostyles, and a more pointed lingual margin. UCM 57499 is about 4% larger in linear dimensions than SDSNH 60872. The M1–2 in MPM 6717 (Figure 1C) are very similar in size and general morphology to the M1–2s from the Friars Formation but differ slightly in having more wrinkled enamel and stronger mesostyles. The M3 in YPM 37189 (Figure 1A) differs from the Friars Formation M3 (UCMP 104316; Figure 1F) in having a smaller metaconule and in being more anteroposteriorly compressed.

The minor differences noted above between the upper molars from the Friars and Bridger formations cannot be ascribed to taxonomic differences at this time, as some variability is evident within the Bridger sample. For example, the M1–2 in MPM 6717 differ from the homologous teeth in UCM 57498 and 57499 in being smaller, in having a more blunt lingual margin, in having weaker conules but stronger hypocones, and in having more wrinkled enamel. The M2 in MPM 6717 also differs from the M2 in YPM 37189 in being wider posteriorly than anteriorly, in having more wrinkled enamel, and in being relatively shorter in anteroposterior length. Samples of *A. venustus* from the Bridger Formation and Friars Formation remain inadequate to determine confidently the true range of morphological and size variation present in each population, and there is no convincing evidence to suppose that these two populations should be assigned to different species.

Discussion.—Golz and Lillegraven (1977, table 1) listed a record of “*Diacodexinae?*” from the Friars Formation. This occurrence was based on LACM 56127, an isolated m3 here referred to *Antiacodon venustus*. The additional Friars Formation specimens of this species, described above, were previously identified as “*Antiacodon* sp. 1” by Walsh (1996:86). Their refined identification here as *Antiacodon venustus* extends the known geographic range of this species from Wyoming to southern California and the known temporal range into the early Uintan.

West (1973:150) assigned several specimens in the UW collection to *Antiacodon pygmaeus*. However, two of these specimens (UW 1519, L dentary fragment with damaged p4–m1; UW 1556, RM3) are quite large (Table 2), and are here tentatively referred to *A. venustus* on this basis. If correct, these re-identifications would extend the temporal range of this species into the early Bridgerian, given West’s (1973) “Bridger B” correlation of UW Locality V-57001 (“Big Sandy”). In numerical terms, the apparent temporal range

TABLE 2. Measurements (in mm) of cheek teeth of *Antiacodon venustus* from the Bridger Formation. Asterisks indicate minimum values because of slight damage, enamel dissolution, or interdental wear.

	P4		M1			M2			M3		
	W	L	AP	AW	PW	AP	AW	PW	AP	AW	PW
YPM 16861	4.17	5.53	—	—	—	—	—	—	—	—	—
MPM 6717	—	—	5.02*	—	6.00	5.15	6.61	6.80	—	—	—
UCM 57498	—	—	—	—	6.22	—	—	—	—	—	—
UCM 57499	—	—	—	—	—	5.62	6.97	7.02	—	—	—
YPM 37189	—	—	—	—	—	5.35	6.59	6.64	4.30*	6.08	5.05
UW 1556	—	—	—	—	—	—	—	—	4.12*	—	5.24
Mean	—	—	—	—	6.11	5.37	6.72	6.82	4.22	—	5.15

	p4		m1			m2			m3		
	AP	W	AP	WTRI	WTAL	AP	WTRI	WTAL	AP	WTRI	WTAL
YPM 13271	6.26*	3.47	—	3.47	—	—	—	—	6.75*	—	—
YPM 13272	5.77	3.46	4.98	3.67	3.70	5.70	3.96	4.34	—	—	—
YPM 16861	—	—	5.15	3.54	4.12	5.44	3.95*	4.70	6.21	4.00	3.72
YPM 37188	—	—	5.23	3.20	3.55	—	—	—	—	—	—
YPM 13273	—	—	—	—	—	5.22	3.92	4.28	—	—	—
YPM 13277	—	—	—	—	—	—	—	4.41	6.30	3.68	3.60
YPM 11765 (type)	—	—	—	—	—	—	—	—	6.2 ^a	3.66*	3.58
USNM 13446	—	—	5.37	3.63	4.17	—	—	—	—	—	—
USNM 364903	—	—	—	—	—	—	—	—	6.11	3.59	3.47
UW 1519	5.23	3.62	5.08*	3.26	3.74*	—	—	—	—	—	—
Mean	5.75	3.52	5.16	3.46	3.86	5.45	3.94	4.43	6.31	3.73	3.59

^aMeasurement from Marsh (1872:211). The hypoconulid of YPM 11765 is damaged, and the tooth currently measures only 6.04 mm in anteroposterior length.

(parachron of Walsh, 1998) of *A. venustus* is determined by the putative oldest known record (OKR) as represented by the specimens from UW V-57001 (about 48 million years ago [Ma] based on a new ⁴⁰Ar/³⁹Ar date from Bridger B reported by Murphey et al., 1999) and the putative youngest known record (YKR) as represented by the stratigraphically highest specimens described above from the Friars Formation (very roughly 45 Ma according to the magnetostratigraphic correlations of Walsh et al., 1996, as modified here). Thus, the parachron of *A. venustus* is about 3 million years.

The only specimen from Bridger B assigned to *A. venustus* by West (1984:44) was YPM 13274, a "batched" specimen lot which includes an artiodactyl dentary fragment with worn m1–3, unworn and probably associated LM1 or 2 and LM3 of a small artiodactyl, an M2 of *Hyopsodus* sp., and an M1 of the rodent *Sciuravus*. The lower molars in the dentary fragment are distinctly smaller than the other teeth of *A. venustus* in the YPM collection and are about the size of those of *A. pygmaeus*. However, the cristid obliqua is quite weak and is directed toward the area between the protoconid and metaconid, rather than to the metaconid. The lower jaw fragment in YPM 13274 is therefore probably referable to *Microsus* or a small species of *Homacodon*. The M1 and M3 included in YPM 13274 differ from *Antiacodon* in their lack of a mesostyle and anterocone and in their stronger hypocones. The size and morphology of these upper molars are entirely consistent with the figures and descriptions of *Microsus cuspidatus* given by West (1984). YPM 37192 (L dentary fragment with m1–2), assigned by West (1984:44) to *A. pygmaeus*, also pertains to *Microsus*.

Stucky (1998:366) suggested that the type and only known specimen of *Neodiadocodex emryi* (see West and Atkins, 1970, and below) might represent the upper dentition of *A. venustus*. However, as discussed above, P4–M3 of Bridger Formation *A. venustus* are known from YPM 16861, YPM 37189, MPM 6717, and UCM 57498–57499. The P4 in YPM 16861 is only slightly smaller than the P4 in the type of *N. emryi* but differs morphologically from the latter in its lack of a distinct cusplule on the posterior cingulum and its smooth rather than crenulated enamel. The M2 in YPM 37189 and the

M1–2 of UCM 57498 and 57499 differ from the M1–2 of *N. emryi* in having smooth rather than crenulated enamel, having more conical conules with weaker conular wings, lacking an accessory cusp on the postcingulum, lacking a lingual cingulum (nearly complete in *N. emryi*), and in having more pointed lingual margins (as opposed to the blunt lingual margins of M1–2 in *N. emryi* caused by the lingual expansion of the cingular hypocone). Given these differences, it may be concluded that the type specimen of *Neodiadocodex emryi* does not represent the upper dentition of *Antiacodon venustus*.

Tapochoerus McKenna, 1959

Type Species.—*Tapochoerus egressus* (Stock, 1934a).

Included Species.—*Tapochoerus mcmillini* sp. nov.

Diagnosis.—Differs from *Antiacodon* and *Auxontodon* in having upper molars that lack mesostyles, generally lack anterocones, and that have weaker, discontinuous labial cingula. Also differs from these two genera in its lack of a metaconid on p3 and in having a paraconid partly to completely merged with the metaconid on m2–3. Further differs from *Auxontodon* in having a slightly rather than strongly convex ventral border of the dentary. Differs from *Neodiadocodex* in its lack of a cusplule on the posterior cingulum of P4 and its lack of mesostyles, anterocones, and crenulated enamel on the upper molars.

Known Distribution.—Late Uintan (middle middle Eocene) of southern California. Middle member of Sespe Formation, Ventura County. Member C of Santiago Formation, Mission Valley Formation, and Miramar Sandstone Member of Pomerado Conglomerate, San Diego County.

Tapochoerus egressus (Stock, 1934)

Figure 6

Diagnosis.—Linear measurements of cheek teeth ranging from 14% to 47% larger than those of *Tapochoerus mcmillini* sp. nov.; P4 with stronger cingula and preprotoconista than in *T. mcmillini*; upper

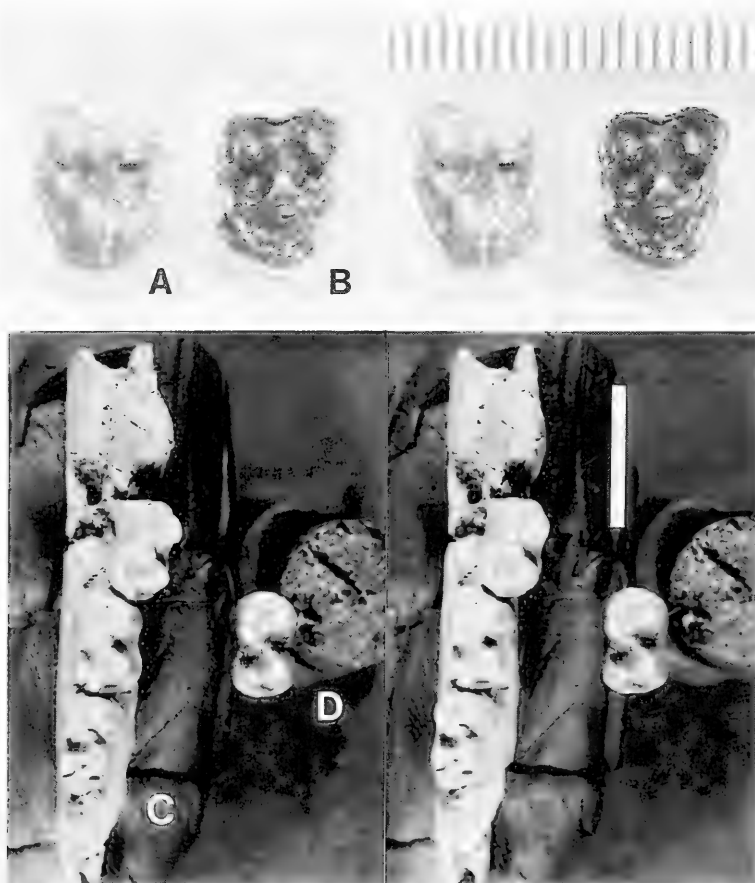


Figure 6. Stereophotographs in occlusal view of teeth of *Tapochoerus egressus* from California: (A), SDSNH 62198, LM2, member C of Santiago Formation, San Diego County; (B), LACM (CIT) 1598, RM2, middle member of Sespe Formation, Ventura County; (C), Cast of LACM (CIT) 1590 (holotype of *T. egressus*), R dentary fragment with p4–m3, middle member of Sespe Formation, Ventura County; (D), SDSNH 62199, Rm1 or 2, member C of Santiago Formation, San Diego County. Scale divisions for A and B in mm; scale bar for C and D = 10 mm.

molars slightly less transverse than in *T. mcmillini*, with distinct gap between protocone and metaconule; hypoconulid of m3 relatively shorter than in *T. mcmillini*.

Referred Specimens.—SDSNH 4081/62198 (LM2) and 4082/62199 (Rm1 or 2). Both localities (Emerald Ridge East sites 1 and 2, respectively) were collected from the upper part of member C of the Santiago Formation in Carlsbad, northwestern San Diego County, California.

Description.—The M2 is complete and slightly worn (Figure 6A). The paracone and metacone are conical, equal in height and diameter, and connected by a weak centrocrista. A weak parastyle and metastyle are present. The ectoflexus is quite deep, and a relatively weak ectocingulum is present along the labial border of the tooth but is interrupted at the labial base of the paracone. There is no distinct mesostyle. A strong anterior cingulum extends from the anterolabial base of the protocone to the parastyle, but a continuous

lingual cingulum is absent. A very weak anterocone is present as a slight swelling of the anterior cingulum at the base of the “gully” between the paraconule and protocone. The protocone is conical and is connected to the strong paraconule by a short preprotocrista. The paraconule in turn bears short pre- and postparaconular wings, which extend to the lingual base of the paracone. A strong metaconule is present, separated by a gap from the protocone. The metaconule bears short pre- and postmetaconular wings, which extend to the lingual base of the metacone. The small distinct hypocone is conical and sends a posterior cingulum to connect with the metastyle. Measurements of SDSNH 62198 (mm): AP = 7.90; AW = 10.07; PW = 9.92.

The m1 or 2 is complete and unworn, with the exception of slight damage to the hypoflexid area (Figure 6D). The lingual and labial outlines of the tooth are both distinctly concave in occlusal view. An anterior cingulum extends from the anterior base of the paraconid to the anterior base of the protoconid. The conical protoconid is by far

the largest trigonid cusp. The conical paraconid is located directly anterior to the conical metaconid. The paraconid is subequal to the metaconid in size but slightly taller than the latter cusp. The trigonid is enclosed anteriorly by a distinct paralophid and posteriorly by a weaker metalophid. The hypoconid is by far the largest talonid cusp and sends a strong cristid obliqua high up the postvallid, which ends just short of the metaconid apex. The twinned entoconid and hypoconulid are subequal in height and diameter. A wide postcingulid extends from the hypoconulid to the posterior base of the hypoconid. The talonid is open lingually, with a tiny cuspid in the talonid notch. Measurements of SDSNH 62199 (mm): AP = 7.76; WTRI = 4.83; WTAL = 4.88.

Comparisons.—*Tapochoerus egressus* was previously known only from the Sespe Formation of southern California, where it is represented by several specimens from the Tapo Canyon and Brea Canyon local faunas (McKenna, 1959; Kelly, 1990). SDSNH 62198 is quite similar in size and morphology to LACM (CIT) 1598 (Figure 6B), an M2 of *T. egressus* described by Stock (1934) and McKenna (1959). SDSNH 62198 differs from LACM (CIT) 1598 in lacking a continuous lingual cingulum and in having stronger pre- and postmetaconular wings, a deeper ectoflexus, and a slightly larger hypocone. The development of the lingual cingulum is highly variable in upper molars of *T. egressus* from LACM (CIT) 180. For example, LACM (CIT) 1598 (M2), LACM 40534 (M2), and LACM (CIT) 5227 (M3) have a strong, complete lingual cingulum, while LACM 40537 (M1), LACM (CIT) 5226 (M1), 1597 (M1 or 2), 5230 (associated M2–3; see McKenna, 1959: plate 37A), and LACM 40538 (M3) all lack a continuous lingual cingulum. SDSNH 62198 and the M1–2s from LACM (CIT) 180 consistently have a weak ectocingulum with a distinct interruption at the labial base of the paracone (McKenna, 1959:128).

SDSNH 62199 is very similar in morphology to the m1–2s in LACM (CIT) 1587, 1588, 1589, and 1590 (see Stock, 1934), which are dentary fragments of *T. egressus* from the Tapo Canyon local fauna of the Sespe Formation (Figure 6C). SDSNH 62199 is distinctly longer in AP length than the m1s in these four Sespe jaws (means are 7.24 mm, 4.75 mm, and 4.93 mm for AP, WTRI, and WTAL, respectively). SDSNH 62199 is more similar in AP length to the m2s in these four jaws (means are 7.69 mm, 5.16 mm, and 5.25 mm for AP, WTRI, and WTAL, respectively), but the Santiago Formation lower molar is more transversely compressed than the Sespe

m2s. Therefore, SDSNH 62199 is identified only as an m1 or 2.

Discussion.—The minor morphological differences between the Sespe Formation and Santiago Formation specimens cannot be regarded as taxonomically significant given the small sample size available from the latter unit. The two isolated molars described above represent the first record of *Tapochoerus egressus* from San Diego County, thus increasing the number of species known from late Uintan strata of both San Diego and Ventura counties (Walsh, 1996, table 3). The ages of SDSNH Locs. 4081 and 4082 (which were probably collected from the same fossiliferous bed exposed along strike) are not known with sufficient precision to determine their age relative to the Tapo and Brea Canyon local faunas of the Sespe Formation. However, it is interesting to note that these now-destroyed localities occurred at least 60 m above the local base of member C of the Santiago Formation (unpublished stratigraphic section in B. O. Riney Notebook # 24, on file at SDSNH). SDSNH Locs. 4081 and 4082 have also yielded several specimens of the protoceratid artiodactyl *Leptoreodon leptolophus*, a species which is otherwise confidently known in San Diego County only from the latest Uintan or early Duchesnean Laguna Riviera local fauna (Golz, 1976) and the faunally similar and geographically proximate SDSNH Loc. 3495 (Walsh, 1996:92). SDSNH Locs. 4081 and 4082 thus appear to be somewhat younger than certain other late Uintan assemblages from member C in northern San Diego County, such as the Jeff's Discovery and Rancho del Oro local faunas discussed by Walsh (1996).

Tapochoerus mcmillini sp. nov.

Figures 7–9A

Type Specimen.—SDSNH 3870/54400, R maxillary fragment with P3–M3. Mission Valley Formation, late Uintan.

Referred Specimens, Santiago Formation, Member C.—Jeff's Discovery local fauna (SDSNH Locs. 3276, 3562, and 3564): SDSNH 52238 and 52390 (RM1s). SDSNH 52973 (RM2). SDSNH 47644, L dentary fragment with m1–3. SDSNH 52971, L dentary fragment with m1. SDSNH 47457 (Rm1?) and 52717 (Lm1?). SDSNH 52972, Lm2.

Mission Valley Formation.—SDSNH 3870/54592, RM2. UCMP V-6893/96247, RM3.

Miramar Sandstone Member of Pomerado Conglomerate.—SDSNH 4448/72388, LM1 fragment.

TABLE 3. Measurements (in mm) of cheek teeth of *Tapochoerus mcmillini* from the late Uintan of San Diego County. Asterisks indicate minimum values because of slight damage, enamel dissolution, or interdental wear.

	P3		P4		M1			M2			M3		
	AP	W	AP	W	AP	AW	PW	AP	AW	PW	AP	AW	PW
SDSNH 52238	—	—	—	—	5.49	6.51	6.64	—	—	—	—	—	—
SDSNH 52390	—	—	—	—	5.49	6.45	6.63	—	—	—	—	—	—
SDSNH 52973	—	—	—	—	—	—	—	5.21	7.07	6.97	—	—	—
SDSNH 54592	—	—	—	—	—	—	—	5.42	6.97	6.91	—	—	—
SDSNH 54400 (type)	7.38	4.47	5.33	6.44	5.65*	6.65*	6.89*	5.59*	—	—	4.44*	6.22*	6.09*
UCMP 96247	—	—	—	—	—	—	—	—	—	—	4.58	6.15	5.54
Mean	—	—	—	—	5.54	6.54	6.72	5.41	7.02	6.94	4.51	6.19	5.72
	m1			m2			m3						
	AP	WTRI	WTAL	AP	WTRI	WTAL	AP	WTRI	WTAL				
SDSNH 47457	5.50	3.67	3.71	—	—	—	—	—	—				
SDSNH 52717	5.73	3.64	3.72	—	—	—	—	—	—				
SDSNH 52971	5.65	3.78*	3.87	—	—	—	—	—	—				
SDSNH 47644	5.60	3.74	3.72	5.73	4.00	4.23	6.43	4.07	—				
SDSNH 52972	—	—	—	5.64	4.22	4.15	—	—	—				
Mean	5.62	3.71	3.76	5.69	4.11	4.19	—	—	—				

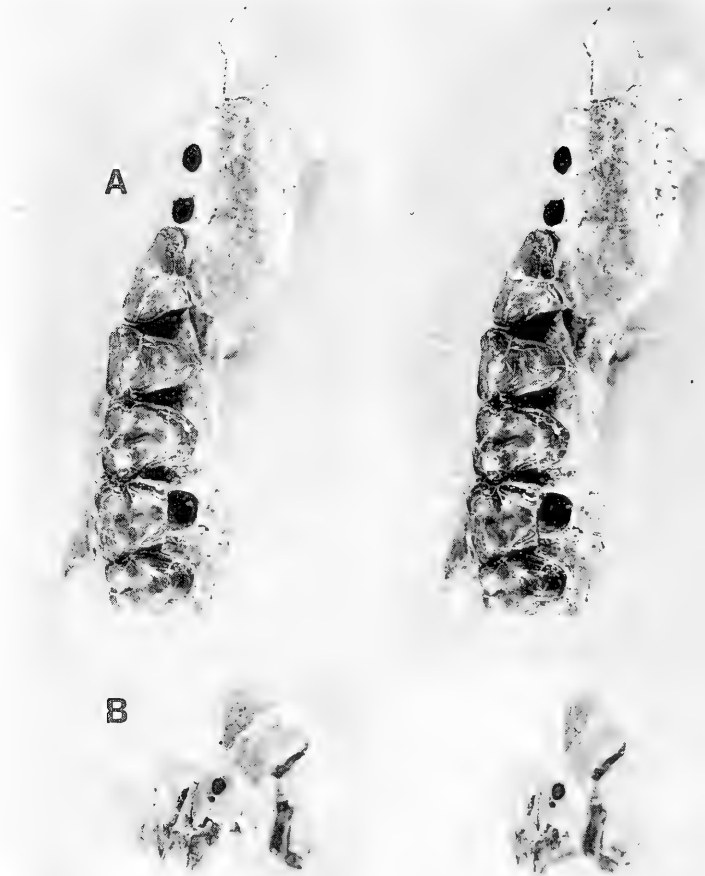


Figure 7. Stereophotographs of SDSNH 54400, R maxillary fragment with partial P1 alveolus, alveoli for P2, and P3–M3, holotype of *Tapochoerus mcmillini* sp. nov.: (A), Occlusal view; (B), Oblique anterior view showing double infraorbital foramina dorsal to anterior root of P3, and cross-section of broken posterior alveolus for P1. Both scale bars = 10 mm.

Diagnosis.—Linear measurements of cheek teeth ranging from 12% to 32% smaller than those of *Tapochoerus egressus* (Table 3); P4 with weaker cingula and weaker preprotocrista than in *T. egressus*; upper molars slightly more transverse than in *T. egressus* and without distinct gap between protocone and metaconule; hypoconulid of m3 relatively larger than in *T. egressus*.

Etymology.—Species named for Mr. Corky McMillin of McMillin Communities, who provided support for palaeontological mitigation above and beyond the call of duty during the grading of various phases of the Scripps Ranch North housing development between 1990 and 1995.

Description.—The holotype maxilla (SDSNH 54400) has two infraorbital foramina directly dorsal to the anterior root of P3 (Figure 7B). The larger, more dorsal foramen is elliptical in outline, 1.9 mm in dorsoventral diameter, and 1.3 mm in lateral diameter. Immedi-

ately ventral to this foramen is a smaller circular foramen 0.6 mm in diameter. No other cranial structures are discernible.

SDSNH 54400 preserves part of the alveolus for a long, narrow root that is presumably the posterior root of a double-rooted P1 (Figures 7A–B). That P1 in *T. mcmillini* was probably double-rooted is suggested by LACM (CIT) 5233, a very high-crowned, triangular, double-rooted tooth from LACM (CIT) Loc. 180 that was tentatively assigned to *T. egressus* by McKenna (1959:126). I agree that this tooth probably pertains to *T. egressus*, and further suggest that it is almost certainly a P1, as the P2 of most early artiodactyls tends to be distinctly lower-crowned than the P1. To my knowledge, P1 is not preserved in place on any available artiodontine specimen. However, a double-rooted, high-crowned P1 is present in bunodont forms such as *Helohyus milleri* (described as *Lophiohyus alticeps*; see Sinclair, 1914: fig. 9; Stucky, 1998:369) and *Diacodexis pakistan-*

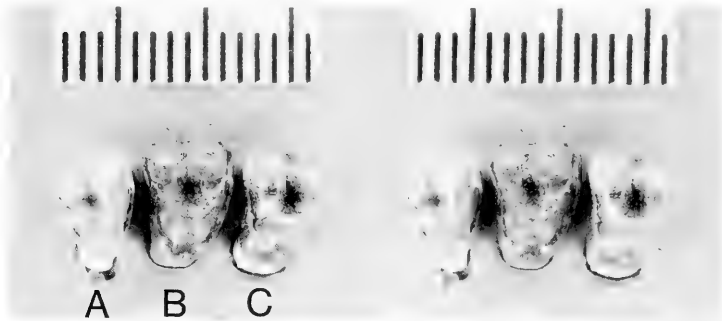


Figure 8. Stereophotographs in occlusal view of composite referred RM1-3 of *Tapochoerus mcmillini*: (A), UCMP 96247, M3; (B), SDSNH 52973, M2; (C), SDSNH 52238, M1. Scale divisions in mm.

ensis (see Thewissen et al., 1983: plate 1, fig. 3a), as well as selenodont forms such as *Leptoreodon* (see Wortman, 1898: fig. 1) and *Hypertragulus* (see Scott, 1940, plate LIV). The P1 is also double-rooted but relatively low-crowned in *Protylopus petersoni* (see Wortman, 1898: fig. 3), *Homacodon vagans* (crown height unknown; see Sinclair, 1914: fig. 19), *Stibarus yoderensis* (see Macdonald, 1955), *Gobiohyus orientalis* (see Coombs and Coombs, 1977a), and *Messelobunodon* (see Franzen, 1983: plate 2, fig. 3). There is a diastema of 7 mm between the posterior edge of the posterior alveolus for P1 and the anterior edge of the anterior alveolus for P2. The distance between the anterior edge of the anterior alveolus of P2 and the posterior edge of the posterior alveolus of P2 is 5.9 mm. There is no diastema between P2 and P3.

P3 and P4 are known only from the holotype (Figure 7A). P3 is large and anteroposteriorly elongate, with a strong parastylar lobe,

and a weak ridge connecting the anterior flank of the paracone to the weak parastyle. The paracone dominates the crown and is the tallest cusp of any on the upper cheek teeth. There is a fairly strong metastylar crest, atop which sits a very small metacone. The metastyle is very weak and sends a short cingulum labiad to end at the posterolabial base of the crown. There is no ectocingulum or hypocone. The protocone lobe is very weak, and the protocone is merely the lingual end of the posterior cingulum that connects the metastyle to the protocone lobe. The tooth is triple-rooted, with all roots cylindrical and subequal in diameter.

The P4 has a strong conical paracone with a weak anterior crest that stops just short of the distinct parastyle. A weak anterior cingulum extends from the parastyle toward the lingual base of the protocone but is not complete. The anterior cingulum bears a small indistinct cusplike immediately below the valley between the paracone

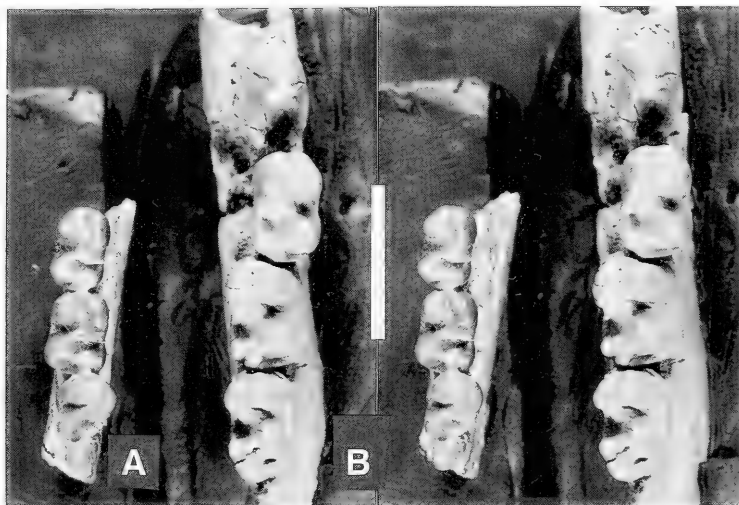


Figure 9. Stereophotograph in occlusal view of (A), SDSNH 47644, referred specimen of *Tapochoerus mcmillini*, L dentary fragment with m1-3; (B), Cast of LACM (CIT) 1590, holotype of *T. egressus*, R dentary fragment with p4-m3. Scale bar = 10 mm.

and protocone. There is a weak metastylar crest on the posterior flank of the paracone that extends to the weak metastyle. There is no ectocingulum, although the enamel along the base of the crown is partially dissolved. A strong posterior cingulum extends from the metastyle to the lingual base of the protocone. There is no hypocone. The protocone is strong and conical, with no pre- or postprotocristae. The tooth is triple-rooted, with the lingual root being the largest.

M1 in the holotype is lightly worn. The paracone and metacone are conical and equal in diameter, but the metacone is slightly taller than the paracone. There is no distinct parastyle or metastyle. The labial base of the metacone extends slightly further labially than the labial base of the paracone. A weak ectocingulum is present only between the labial faces of the paracone and metacone, and there is no mesostyle. The protocone is essentially conical and is connected to the conules by weak pre- and postprotocristae. The conular wings are generally weak, with the premetaconular wing being the strongest. Strong anterior and posterior cingula are present but stop just short of connecting around the lingual base of the protocone. The anterior cingulum ends lingually in a tiny anterocone, while the postcingulum ends in a small but distinct hypocone. The lingual base of the anterocone extends slightly further lingually than the lingual base of the hypocone. SDSNH 52238 (Figure 8C) is similar to the M1 in SDSNH 54400 except that the anterior cingulum does not extend as far lingually; there is no anterocone, and the base of the hypocone extends slightly further lingually than the base of the protocone. The single fragmentary M1 from the Miramar Sandstone Member of the Pomerado Conglomerate (SDSNH 72388, not figured) is very similar to the M1 in the holotype, although no standard measurements can be taken.

The M2 in the holotype is missing the lingual third of the crown but is similar in size and general morphology to M1. SDSNH 52973 (Figure 8B) is an isolated, essentially unworn M2. It confirms that M2 is similar to M1 in having a weak, discontinuous ectocingulum and no mesostyle. Unlike M1, the labial base of the paracone extends slightly further labially than the labial base of the metacone, and the paracone is slightly taller than the metacone. M2 also differs from M1 in its lack of a hypocone and anterocone.

The M3 in the holotype is abraded, and its labial face is slightly damaged. The metacone is shorter than the paracone, and the conules are weaker than in M1–2. The anterior and posterior cingula are just as strong as in M1–2 but are less continuous around the lingual flanks of the protocone. There is no hypocone or anterocone.

An isolated M3 referable to *T. mcmillini* is known from a Mission Valley Formation locality in the La Mesa area. UCMP 96247 (Figure 8A) is complete and well-preserved, with only the paracone showing minor wear. The tooth is essentially triangular in occlusal outline, with a large cylindrical lingual root, and two smaller cylindrical labial roots. The presence of a distinct anterior appression facet and the absence of a posterior appression facet confirm the tooth to be an M3. The paracone is conical, distinctly taller than the conical metacone, and located well labial to the metacone. A weak rib extends down the anterior face of the paracone to the parastylar area, although there is no distinct parastyle. A weak centrocrista connects the paracone and metacone. There is no labial cingulum, no mesostyle, and no metastyle. A small paraconule is present, but it occurs atop the preparaconular wing, not at the junction of the pre- and postparaconular wings. A very weak metaconule occurs at the junction of the pre- and postmetaconular wings. The protocone is broad, lower than the two labial cusps, and sends distinct pre- and postprotocristae labially toward the conular wings. There is no hypocone. Distinct anterior and posterior cingula are present but not continuous around the lingual base of the protocone and are distinctly weaker than the cingula in the M3 of the holotype. Finally, UCMP 96247 has a more pointed lingual margin than the M3 in the holotype.

SDSNH 47644 (Figure 9A) is a dentary fragment with m1–3. It is 8.7 mm deep below the m2–m3 contact. The m1 has a conical protoconid and metaconid. The paraconid is slightly transversely compressed but equal in size to and well separated from the metaconid. A weak paralophid extends from the paraconid to the anterior face of the protoconid, and a weak metalophid connects the metaconid with the lingual base of the protoconid. There is a short weak anterior cingulid. A strong cristid obliqua extends up toward the metaconid apex. There are three tiny cusplids in the hypoflexid. The deep talonid notch opens lingually. The hypoconid is strong. The hypoconulid and entoconid are well worn but much smaller than the hypoconid. There is a short but wide posterior cingulid. SDSNH 52717 (m1?) is similar in size and proportions to the m1 in SDSNH 47644 but has a partially fused paraconid and metaconid, as in m2 of the latter specimen. In contrast, SDSNH 47457 (m1?) is similar in size and proportions to the m2 in SDSNH 47644 but has a conical paraconid well separated from the metaconid.

The m2 in SDSNH 47644 is similar to m1 but is slightly larger, less transversely compressed overall, and has a more transversely compressed paraconid that is not well separated from the metaconid. The hypoconulid is small and equal in size to the hypoconid. SDSNH 52972 is an isolated m2 that differs from the m2 in SDSNH 47644 in having a trigonid wider than the talonid. SDSNH 52972 also has a partially fused paraconid and metaconid, and the hypoconulid is taller than the entoconid.

The m3 in SDSNH 47644 has the paraconid completely fused with the metaconid. The resulting transversely compressed loph turns anteriorly into a strong paralophid that extends to the anterior base of the protocone. The hypoconulid is relatively large, but the entoconid area is damaged.

Comparisons.—The specimens described above were initially identified as “*Antiacodon?* sp. 2” by Walsh (1996:86). Although the teeth are about the same size as those of *A. venustus* from the Friars Formation, they differ significantly from both *Antiacodon* and *Auxontodon* in their lack of mesostyles and anterocones and in the progressive fusion of the metaconid with the paraconid from m1–3. In these features and in their weak, discontinuous labial cingula, the specimens closely resemble *Tapochoerus egressus*. In addition to being significantly smaller, *T. mcmillini* differs morphologically from *T. egressus* in that an isolated P4 probably referable to the latter species (LACM 40548, not figured; originally identified by D. J. Golz) has relatively stronger anterior and posterior cingula, a complete lingual cingulum, a weak complete ectocingulum, and a stronger preprotocrista than the P4 in the holotype of *T. mcmillini*. Upper molars of *T. mcmillini* also appear to be slightly more transverse than those of *T. egressus*. More importantly, upper molars of *T. mcmillini* lack a distinct gap between the protocone and metaconule, unlike *T. egressus* and all other known antiacodontines. Finally, the single known m3 of *T. mcmillini* (in SDSNH 47644) has a relatively long hypoconulid lobe compared to the short hypoconulid lobes in all known m3s of *T. egressus*.

Tapochoerus mcmillini is similar to the Wasatchian genus *Hexacodus* in lacking mesostyles and in having a joined or closely appressed paraconid and metaconid on m2–3 (see Gazin 1952: plate 11; Gazin, 1962: plate 7, fig. 2; plate 14, fig. 1). However, *T. mcmillini* differs from *Hexacodus* in having the antiacodontine condition of the cristid obliqua and a much larger and morphologically “standard” primitive artiodactyl P3 (Gazin, 1962: plate 7, fig. 2; Stucky, 1998: fig. 23.3F), in lacking a distinct gap between the protocone and metaconule (Gazin, 1962: plate 14, fig. 1), in having an M3 relatively smaller than M1–2 (Stucky, 1998: fig. 23.3F), in having relatively narrower lower molars, and in having a larger hypoconulid lobe on m3 (Gazin, 1952: plate 11, figs. 2–3). The p4 of *Hexacodus* is very distinctive (Gazin, 1952: plate 11, fig. 1; Krishtalka and Stucky, 1986:

fig. 7), but this tooth is not preserved in the available sample of *T. mcmillini*.

Tapochoerus mcmillini is very similar in upper molar morphology to *Diacodexis*, especially in the lack of a distinct gap between the protocone and metaconule. However, *T. mcmillini* differs from *Diacodexis* in having a relatively smaller M3, lower molars relatively more elongated anteroposteriorly, and a paraconid completely merged with the metaconid on m3 (see various figures in Krishtalka and Stucky, 1985).

The double infraorbital foramina of *Tapochoerus mcmillini* are interesting features, but this part of the snout is not preserved in available specimens of *T. egressus*. The infraorbital foramina of SDSNH 54400 are located dorsal to the anterior root of P3 as in *Antiacodon pygmaeus* and *Diacodexis*, but in these taxa the infraorbital foramen is reportedly single rather than double (West, 1984:8). The skull of *Diacodexis pakistanensis* described by Russell et al. (1983) apparently also has a single infraorbital foramen, as does the skull of *Messelobunodon* described by Franzen (1981). Interestingly, SDSM 3375 (specimen not seen; assigned to *Stibarus obtusilobus* by Scott, 1940, plate XXXVII; regarded as the type of *Nanochoerus scotti* by Macdonald, 1955; reassigned to *Leptochoerus elegans* by Edwards, 1976:111) reportedly has a double infraorbital foramen, with both foramina apparently being subequal in size (Scott, 1940:373). In contrast, Scott (1940:377) reported that the infraorbital foramen in Amherst College 1787 (specimen not seen; assigned by him to the new leptochoerid species *Stibarus loomisi*; assigned to *S. quadricuspis* by Edwards, 1976) is "narrow and slitlike and opens above the space between P2 and P3." The phylogenetic significance of the double infraorbital foramen in *Tapochoerus mcmillini* is uncertain given our poor knowledge of the status of this character in other taxa.

Discussion.—The holotype maxilla of *T. mcmillini* is from the late Uintan Mission Valley Formation, whereas all known lower molars of this species are from member C of the Santiago Formation (late Uintan Jeff's Discovery local fauna). Nevertheless, several isolated upper molars from Jeff's Discovery are indistinguishable from those in the holotype; this provides strong evidence that the hypodigm listed above pertains to a single species.

The specimens of *T. mcmillini* from the Jeff's Discovery local fauna (basal part of member C of the Santiago Formation) and the Mission Valley Formation are evidently older than the specimens of

T. egressus described above from the upper part of member C of the Santiago Formation. The possibility of an ancestor–descendant relationship between the two species cannot be entirely ruled out, but *T. mcmillini* does possess a potential autapomorphy in its unexpected lack of a distinct gap between the protocone and metaconule. This *Diacodexis*-like condition in *T. mcmillini* may represent a derived reversion to a generally more primitive character state.

Because the Jeff's Discovery local fauna, SDSNH Loc. 3870, and UCMP Loc. V-6893 are indistinguishable in terms of relative age, the parachron of *T. mcmillini* is essentially zero. The parachron of *Tapochoerus* is determined by the putative OKR of *T. mcmillini* (about 42.8 Ma, based on a bentonite date from the Mission Valley Formation obtained by J. D. Obradovich; see Walsh, 1996) and the putative YKR of *T. egressus* (about 40.5 Ma, based on the age of the Brea Canyon local fauna as inferred from magnetostratigraphic correlation by Prothero et al., 1996). Thus, the parachron of *Tapochoerus* is about 2.3 million years.

Antiacodontinae, unidentified genus and species Figure 10A

Referred Specimen.—SDSNH 3785/49267 (RM1?), from uppermost part of undifferentiated Friars Formation, early Uintan.

Description.—The tooth is complete and unworn, and relatively wide transversely. The paracone and metacone are tall and conical, with weak centrocristae and weak ridges extending from their apices to the parastyle and metastyle. There is a very weak cuspule where the centrocristae converge (mesostyle?), but the ectocingulum also shows a distinct elevation directly labial to this cuspule. The ectoflexus is moderately deep. The strong paraconule has a strong pre- but a weak postparaconular wing, whereas the strong metaconule has a moderate pre- and a strong postmetaconular wing. The protocone has conical lingual flanks but a nearly planar posterolabial flank. There is a weak connection between the protocone and paraconule but a distinct gap between the protocone and metaconule. There is a small hypocone. The anterocone is just a weak rise of the anterior cingulum, and there is no lingual cingulum. The tooth is three-rooted, with a large cylindrical lingual root and two much smaller labial roots, slightly compressed anteroposteriorly. Some very weak crenulation is present on the flanks of the major cusps. Measurements (mm):

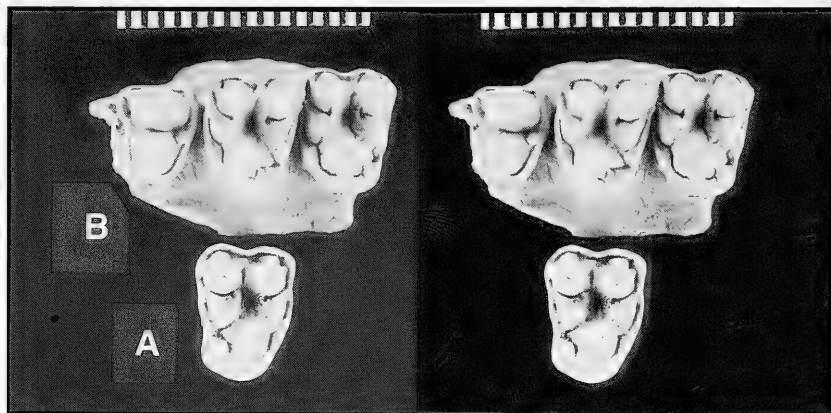


Figure 10. Stereophotograph in occlusal view of: (A), SDSNH 49267, unidentified antiacodontine, RM1? (coated with ammonium chloride); (B), Cast of AMNH 56054, holotype of *Neodiocodexis emryi*, L maxillary fragment with P4–M2. Scale divisions in mm.

AP = 5.90; AW = 7.93; PW = 7.99.

Discussion.—This tooth was originally thought to be an M2 of *Antiacodon venustus*, but inspection of associated M1–2s of *A. venustus* and *A. pygmaeus* reveals that these teeth are generally subequal in size, with M2 only slightly wider transversely than M1 (e.g., MPM 6717 and UCM 57498 and 57499; see also West, 1984, fig. 3; Gunnell, 1998, fig. 20C). In addition, the anterior width of SDSNH 49267 is slightly less than the posterior width; this suggests that this tooth may be an M1. SDSNH 49267 is similar to all antiacodontines (*Tapochoerus mcmillini* excluded) in having a weak connection between the protocone and paracone but a distinct gap between the protocone and metacone. SDSNH 49267 differs from Friars Formation specimens of *A. venustus* in being 9% to 19% larger in linear dimensions than the largest available M1–2s of this species. SDSNH 49267 also has stronger conular wings than all known upper molars of *A. venustus* and is more similar in this respect to the type and only known specimen of *Neodiadocodex emryi* (AMNH 56054; Figure 10B). However, SDSNH 49267 has only very weakly crenulated enamel, lacks a lingual cingulum, and is about 16% wider than the M1 and 8% wider than the M2 of *N. emryi*.

SDSNH 49267 is similar to CM 19785 (an isolated M3 from the late Uintan of Badwater, Wyoming; see Black, 1978:232) in its possession of relatively sharp cusps and crescentic conules. However, CM 19785 has a strong lingual cingulum (absent in SDSNH 49267) and belonged to an animal somewhat larger than the one represented by SDSNH 49267. Black (1978:232) suggested that CM 19785 could pertain to "*Auxontodon gazini*" (presumably meaning *A. patersoni* Gazin), but this tooth is about the same size as the M3 of *Tapochoerus egressus* (see McKenna, 1959:132). Storer (1984a:74) stated that CM 14552 (Black, 1978: fig. 2) and CM 19785 appear to represent *Auxontodon*, and Stucky (1998:365) also implicitly assigned them to *A. patersoni*, but corroboration of these reasonable suggestions requires more material.

SDSNH 49267 differs from *Tapochoerus egressus* in being more transverse, in having weaker cingula, a smaller hypocone, slightly stronger conular wings, and in ranging from about 12% to 29% smaller in linear dimensions. SDSNH 49267 differs from *T. mcmillini* in ranging from 4% to 15% larger in linear dimensions than the largest M1–2s of the latter species, in having a weak mesostyle, in having stronger conules, and in having a distinct gap between the protocone and metacone. Finally, SDSNH 49267 differs from M1–2 of *Auxontodon processus* Storer, 1984a, in being more transverse, in having much weaker conules and a weaker mesostyle, in lacking a connection between the protocone and hypocone, and in lacking a complete lingual cingulum. More material of this taxon must be collected to identify it confidently.

Finally, note that an M2 and M3 from the early Uintan part of the Devil's Graveyard Formation were assigned by Runkel (1988, figs. 24A, B) to an unnamed new species of *Texodon*. However, as Runkel's illustrations show, TMM 42952-60 and 42952-61 are quite different from the M2–3 in the holotype of *T. meridianus* West, 1982, and seem more likely referable to *Antiacodon*, *Auxontodon*, or the indeterminate taxon described above (note the presence of an anterocone and a distinct gap between the protocone and metacone, although Runkel's specimens do appear to be somewhat smaller than homologous teeth of *Antiacodon venustus*). Stucky (1998:365) has already suggested that TMM 41745-1 (a DP4? from the late Uintan Serendipity local fauna assigned to *Texodon meridianus* by West, 1982) may be referable to *Auxontodon*.

Subfamily Helohyinae Gazin, 1955 (from Marsh, 1877)

Remarks.—The subfamily Helohyinae is used here in the restricted sense of Gazin (1955) and Stucky (1998). McKenna and Bell

(1997) included the Asian taxa *Gobiohyus* and *Pakkokuhys* within the family Helohyidae (e.g., Coombs and Coombs, 1977a; Holroyd and Ciochon, 1995), but Stucky (1998:369) suggested that the resemblance of these taxa to North American helohyines was due to convergence. Stucky (1998) proposed that helohyines were part of the basal selododont radiation, but here I adopt an even more conservative approach and leave this subfamily *incertae sedis* within Artiodactyla.

Achaenodon Cope, 1873b

Type Species.—*Achaenodon insolens* Cope, 1873b.

Diagnosis.—Differs from *Helohyus* in having cheek teeth about 100% larger in linear dimensions than the largest known species of this genus (*H. lentus*), in its derived loss of p1, and in its derived loss of the paraconid on m1. Differs from *Parahyus* in having lower cheek teeth at least 15% larger in linear dimensions, in retaining the primitive condition of having relatively unelongated lower molars (and M3), and in its derived loss of a paraconid on m1. Differs from an unnamed helohyine genus (Stucky, 1998) in having cheek teeth about 100% larger in linear dimensions, in its derived loss of p1, apparently derived crowded tooth row, and derived loss of the paraconid on m1. Autapomorphies include large size and loss of the paraconid on m1.

Known Distribution.—Early Uintan (middle middle Eocene) of North America. Washakie and Teepee Trail formations of Wyoming, Uinta Formation of Utah, and Friars Formation of California.

Achaenodon sp. cf. *A. robustus* Osborn, 1883

Figure 11

Referred Specimens. *Conglomerate tongue of Friars Formation.*—SDSNH 3621/55890, fragmentary C1. SDSNH 3737/47730, partial skull with LC1 + P3–M1 + M3, and associated mx and RM3.

Friars Formation undifferentiated.—SDSNH 3784/50566, Lm1. 3784/50578, RM3. SDSNH 3788/54582, R dentary fragment with roots of p3–4, heavily worn and damaged m1–2, roots of m3, plus associated Lp4. SDSNH 3851/54581, R dentary fragment with m2–3.

Description.—SDSNH 47730 is a highly distorted and crushed partial skull containing variably damaged, heavily worn LC1 + P3–M1 + M3 (Figure 11A). The infraorbital foramen is located dorsal to the middle of P3, as in the type skull of *A. robustus* figured by Osborn (1883) and Peterson (1919). C1 is mostly intact but the enamel has been dissolved away. P2 is absent but was apparently double-rooted, as indicated by damaged alveoli that were partially crushed by anteroposterior compression between C1 and P3. There was apparently a diastema about 10 mm long between P2 and P3, although it is possible that this feature is a result of distortion.

The P3 is two-rooted, and its long axis is oriented more nearly parallel to the AP axis of the molars, rather than being distinctly oblique as in the type of *A. robustus*. The crown consists of a single large cusp, and the posterior end is the widest part of the tooth. Weak cingula are present at the labial and lingual bases of the crown, but the anterior and posterior bases of the crown are too worn to tell if cingula were also present there.

The P4 is dominated by a tall conical paracone and a much smaller, conical protocone. There is no metacone, but a small anterocone is located on the anterior cingulum midway between the anterior bases of the protocone and paracone. There appears to be a continuous cingulum around the labial, anterior, and lingual bases of the crown. The anterior occlusal outline is markedly concave, and the posterior occlusal outline is convex. The parastylar lobe is stronger than the metastylar lobe, and the lingual lobe is stronger than that in the P4 of the type of *A. robustus*, as illustrated by Osborn (1883) and Peterson (1919). P4 is apparently three-rooted, with the lingual

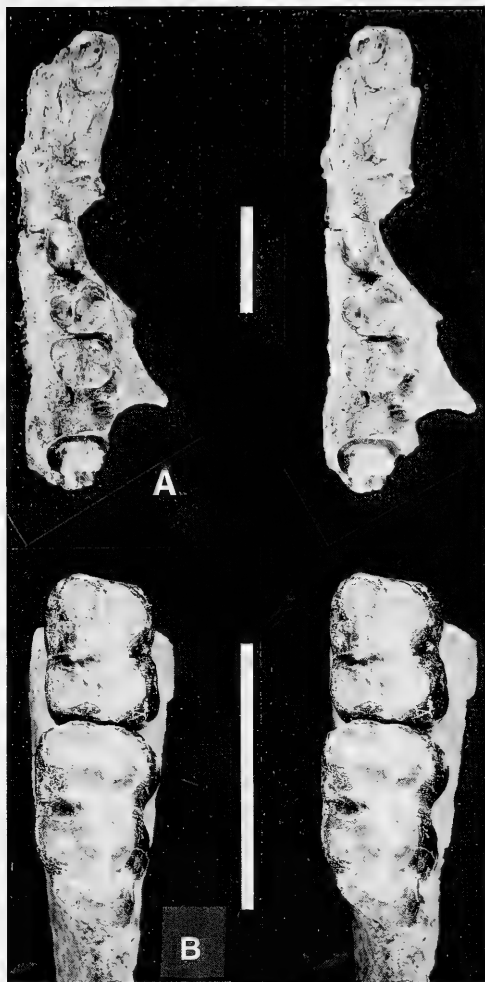


Figure 11. Stereophotographs in occlusal view of specimens of *Achaenodon* sp. cf. *A. robustus* from the Friars Formation: (A), SDSNH 47730, partial skull containing heavily worn LC1 + P3-M1 + M3; (B), SDSNH 54581, R dentary fragment with worn m2-3. Both scale bars = 5 cm.

and anterolabial roots subequal in size. P4 is only slightly worn, whereas M1 is heavily worn, indicating a relatively late time of eruption of P4.

M1 is heavily worn, with no details of the crown discernible. There is a distinct ectoflexus, and the lingual face of the protocone extends further lingual than the lingual face of the hypocone. The tooth is three-rooted, but the lingual root has a distinct lingual bifurcation. The two labial roots are compressed anteroposteriorly. M2 is

missing but, judging from the three alveoli, was distinctly larger than M1, as in the type of *A. robustus*.

M3 is also heavily worn. The hypocone and metacone are much smaller than the protocone and paracone. The labial face of the paracone is heavily worn. A weak posterior cingulum is present below the hypocone but is not continuous around the lingual base of the protocone. The M3 on SDSNH 47730 lacks the posterior cusplule present on the M3 of *A. uintensis*, as illustrated by Peterson (1919, plate XXXIX, fig. 4). Although Peterson's (1919, plate XXXIX, fig. 2) illustration of the M3 of *A. robustus* shows no sign of a posterior cusplule, Osborn's (1883, plate VI, fig. 2) illustration of the same specimen shows a small but distinct cusplule immediately posterolabial to the hypocone. Another isolated, heavily worn M3 from the Friars Formation (SDSNH 50578; not figured) differs from the M3 in SDSNH 47730 in having a continuous ectocingulum but is too worn to tell if a posterior cusplule was present. The lingual root of SDSNH 50578 is transversely compressed, while the labial roots are anteroposteriorly compressed.

The isolated m1 (SDSNH 50566, not figured) is an unworn tooth cap without roots and is identified as such because it is slightly narrower transversely than the m2 in SDSNH 54851. The trigonid is slightly wider than the talonid. The protoconid and metaconid are conical and subequal in size and connected by a weak, anteriorly convex paralophid. There is no paraconid, but a distinct anterior cingulid extends from the anterolabial base of the protoconid to the anterolingual base of the metaconid. A short ridge extends posterolingual from the posterior face of the protoconid to meet the anterior end of the weak cristid obliqua. A similar ridge extends posterolabial from the posterior face of the metaconid but does not reach the cristid obliqua. There is a short labial cingulid in the hypoflexid. The hypoconid and entoconid are conical and subequal in size and connected both by a weak hypolophid and a posteriorly convex postcingulid. There is a small talonid notch between two weak spurs descending from the apex of the entoconid and the posterolingual flank of the metaconid.

The m2-3 in SDSNH 54581 (Figure 11B) are well worn. The m2 is similar in size and morphology to the m1 described above, except that the trigonid is slightly narrower than the talonid, and the spur on the posterior flank of the metaconid is stronger. The latter trend continues in m3, which has a distinct metastylid at the posterolingual base of the metaconid.

A heavily damaged right dentary fragment (SDSNH 54582, not figured) is from an old individual, as shown by the extremely worn m1-2. The dentary is relatively shallow, being only 57 mm deep below the p4-m1 contact and 59 mm deep below the m2-m3 contact. It bears a small mental foramen below the anterior root of p4, and a much larger mental foramen below the anterior root of p3, as in the type specimens of *Achaenodon insolens* (AMNH 5143; see Cope, 1884, plate LVII) and *A. robustus* (see Osborn 1883, plate VI; Peterson 1919, plate XXXIX). SDSNH 54582 also has a short diastema of about 8 mm between p3 and p4, as is also apparently the case in the type of *A. robustus*. The associated Lp4 of SDSNH 54582 (not figured) is complete but heavily worn from occlusion with P4, displaying a deep posterior wear facet similar to that on the p4 of the type of *A. robustus*, as illustrated by Osborn (1883) and Peterson (1919). Table 4 provides dental measurements of *Achaenodon* from the Friars Formation.

Discussion.—Golz and Lillegraven (1977, Table 1) listed a Friars Formation occurrence of "Achaenodontinae?" from LACM (CIT) Loc. 249. This record was based on LACM 55989, a right navicular identified by D. J. Golz. The dental specimens described above confirm the presence of *Achaenodon* in the early Uintan of southern California. Three species of the genus have been recognized. *A. insolens* is known from the middle unit of the Adobe Town Mem-

TABLE 4. Measurements (in mm) of cheek teeth of *Achaenodon* sp. cf. *A. robustus* from the Friars Formation. Asterisks indicate approximate values owing to minor damage.

	P3		P4		M1			M2			M3		
	AP	W	AP	W	AP	AW	PW	AP	AW	PW	AP	AW	PW
SDSNH 47730	25.2*	18.6	21.0*	29.3	22.7*	29.5	25.0*	—	—	—	25.3*	30.0*	—
SDSNH 50578	—	—	—	—	—	—	—	—	—	—	25.2*	27.6	22.8
	p3		p4		m1			m2			m3		
	AP	W	AP	W	AP	TRI	TAL	AP	TRI	TAL	AP	TRI	TAL
SDSNH 54582	—	—	28.3*	19.4	—	—	—	—	—	—	—	—	—
SDSNH 50566	—	—	—	—	27.9	21.4*	19.4	—	—	—	—	—	—
SDSNH 54581	—	—	—	—	—	—	—	28.0	20.8	21.7	37.6	23.7	21.5

ber of the Washakie Formation of Wyoming (McCarroll et al., 1996, table 1) and the Wagonhound Member of the Uinta Formation of Utah (Stucky, 1998). *A. robustus* is known only from the middle unit of the Adobe Town Member of the Washakie Formation (McCarroll et al., 1996, table 1). Finally, *A. uintensis* is known only from the Wagonhound Member of the Uinta Formation (Stucky, 1998). Gazin (1955) questioned whether *A. uintensis* was specifically distinct from *A. robustus* but tentatively retained them as separate species. Prothero (1996) recorded only *A. uintensis* from the Uinta Formation, but Stucky (1998) recorded both *A. uintensis* and *A. insolens* (e.g., Osborn, 1895:105; Peterson, 1919:79–80).

Eaton (1985:355) noted that the P3 in the type skull of *A. robustus* was double-rooted, while the P3 in UW 13991 (assigned by him to *A. sp. cf. A. robustus*) was broader and triple-rooted. The P3 in SDSNH 47730 is double-rooted as in the type of *A. robustus*. The Friars Formation specimens are also similar to *A. robustus* in that they have teeth that are more similar in size to those in the type of *A. robustus* (see Gazin, 1955:40) than to those in the type of *A. uintensis* (see Gazin, 1955:41). However, the dentary of SDSNH 54582 appears to be shallower than the dentaries in the types of *A. insolens* and *A. robustus* and comparable in depth to the dentaries of *A. uintensis* figured by Peterson (1919, fig. 11 and plate XLVII, fig. 4). The Friars Formation specimens are also similar to *A. robustus* in their lack of a posterior accessory cusplule on M3 (absent or weak in the type of *A. robustus*, unknown in *A. insolens*, well-developed in CM 3182, a referred specimen of *A. uintensis*) and in their possession of a short

diastema between p3 and p4 (present in the type of *A. robustus*; absent in the type of *A. insolens* and a referred dentary of *A. insolens* illustrated by Peterson [1919, fig. 11]; absent in a referred dentary of *A. uintensis* figured by Peterson [1919, plate XLVII, fig. 4]; and absent in YPM 19817, a dentary from the Tepee Trail Formation figured and identified as *Parahyus vagus* by Lewis [1973] but re-identified by McKenna [1980] as *Achaenodon* sp.).

Obviously, the populational reality of the above characters is questionable in view of the small sample sizes available of these three nominal species. Nevertheless, the Friars Formation specimens appear to be more similar to *A. robustus* in most characters and so are tentatively compared to this species. It is also worth noting that *A. robustus* Osborn, 1883, has priority over *A. uintensis* Osborn, 1895, should the two names ever be regarded as synonymous.

Parahyus Marsh, 1876

Type and only known species.—*Parahyus vagus* Marsh, 1876.

Diagnosis.—Differs from the largest known species of *Helohyus* (*H. lentus*) in having cheek teeth ranging from 5% to 80% larger in linear dimensions, in its derived loss of p1, and its derived, relatively more elongated m3 and M3. Differs from an unnamed helohyine genus (Snyder, 1993; Stucky, 1998) in having cheek teeth ranging from about 19% to 100% larger in linear dimensions, in its derived loss of p1, its lack of diastemata, and its derived, relatively elongated m3 and M3. Differs from *Achaenodon* in having relatively more elon-

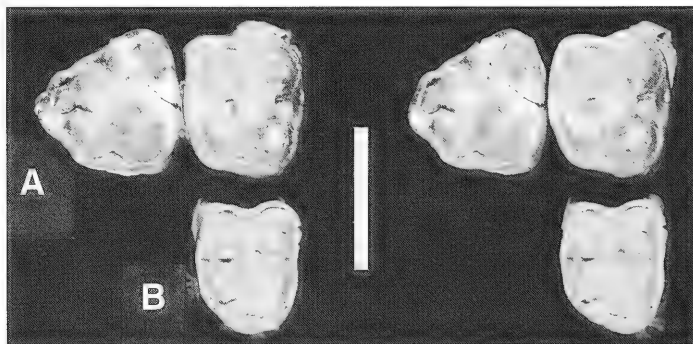


Figure 12. Stereophotograph in occlusal view of: (A), Associated RM2–3 of *Parahyus* sp. from the Friars Formation; (B), Cast of YPM-PU 10027, RM2 of *Helohyus lentus* (holotype of *Parahyus aberrans* Marsh) from Bridger D. Scale bar = 2 cm.

gated lower molars that are at least 15% smaller in linear dimensions, in primitively retaining a paraconid on m1, and in having a relatively elongated m3 and M3. Possible automorphies are the relatively elongated m3 and M3.

Known Distribution.—Early Uintan(?) of Wyoming (Washakie Formation), early Uintan of trans-Pecos Texas (Devil's Graveyard Formation), and early Uintan of southern California (Friars Formation).

Parahyus sp.
Figure 12A

Referred Specimen.—Lower tongue of Friars Formation: SDSNH 3893/55150, associated RM2-3.

Description.—The M2 (Figure 12A) is roughly square in occlusal outline and slightly wider than long. The protocone, paracone, metacone, and hypocone are all conical and subequal in size. There is a distinct conical paraconule fused to the anterolabial base of the protocone, and a weak metaconule seems to have been present. A short anterior cingulum extends from the anterior base of the protocone to the anterior base of the paracone. A strong ectocingulum originates from the anterolabial flank of the protoconule, extends around the labial bases of the paracone and metacone, and merges with a weak postmetacrista at the posterior base of the metacone. There is a distinct ectoflexus in the labial outline of the tooth but no mesostyle. A short spur extends posterolabially from the hypocone apex and ends at the junction of the postmetacrista and posterior cingulum. The latter extends around the lingual base of the hypocone and ends at the posterolingual base of the protocone. The protocone extends much farther linguad than the hypocone, so the lingual outline of the tooth is slightly concave. The apices of the paracone and metacone are slightly worn, while the apices of the protocone and hypocone are moderately worn. The tooth is three-rooted. The lingual root is transversely compressed and slightly larger than the labial roots, both of which are anteroposteriorly compressed. Measurements (mm): AP = 16.3; AW = 20.5; PW = 18.2.

The M3 (Figure 12A) is more anteroposteriorly elongate than M2, with a distinct posterior lobe. The protocone and paracone are the largest cusps and are conical and subequal in size (the posterior flank of the paracone is broken away). A very weak paraconule seems to have been present at the anterolabial base of the protocone. A distinct cingulum is present around the entire circumference of the tooth. The metacone and hypocone are conical and about half the size of the protocone and paracone. A small conical metaconule is fused to the posterolabial base of the hypocone, and another small conical conule is present immediately posterior to the metacone. Moderate wear is evident at the lingual bases of the paracone and metacone and along the anterior cingulum, with only slight wear on the apices of the main cusps. As in the M3 of *Achaenodon*, the lingual and posterolabial roots are subequal in size and transversely compressed, while the anterolabial root is slightly smaller and anteroposteriorly compressed. Measurements (mm): AP = 19.8; AW = 18.9; PW = 15.6.

Comparisons.—SDSNH 55150 formed the basis for Walsh's (1996:86) record of cf. *Parahyus* sp. from the Friars Formation. The M2 of SDSNH 55150 is similar to the M2 of the very large early Uintan helohyid *Achaenodon* (e.g., Peterson, 1919, plate XXXIX) in being essentially square in occlusal outline, with four subequal, conical cusps, a strong paraconule, and a strong ectocingulum. However, SDSNH 55150 is much smaller than *Achaenodon*, having linear dimensions of M2 ranging from only 55% to 64% of those of the M2 of *A. robustus* and *A. uintensis* (see Gazin, 1955:40–41). The M3 in SDSNH 55150 is also grossly similar in morphology to, but distinctly more anteroposteriorly elongated than, known M3s of *Achaenodon*. The SDSNH 55150 M3 has two accessory posterior cusps, while the M3 of *A. uintensis* has a single posterior accessory cusp, and that of

A. robustus has none (Peterson, 1919, plate XXXIX). The M3 in SDSNH 55150 has linear dimensions ranging from only 53% to 74% of those of the M3s of *A. robustus* and *A. uintensis*.

The M2 of SDSNH 55150 is also similar in crown morphology and occlusal outline to Marsh's (1894, fig. 2) type specimen of *Parahyus aberrans* from Bridger D (YPM-PU 10027; figure 12B). YPM-PU 10027 was identified as an M3 by Marsh, but crown proportions and presence of interdental wear facets on both anterior and posterior faces indicate that it is an M2. YPM-PU 10027 was correctly referred to the late Bridgerian taxon *Helohyus lentus* by Gazin (1955:42–43), who described it only as an upper molar. The M2 in SDSNH 55150 ranges from 15% to 18% larger in linear dimensions than YPM-PU 10027 (AP = 14.2 mm; AW = 17.4 mm; PW = 17.3 mm). The latter tooth has a distinct cuspule on the lingual cingulum between the protocone and hypocone that is absent in the SDSNH 55150 M2. Another M2 of *H. lentus* is present in YPM-PU 10084 (Sinclair, 1914, fig. 13; West, 1984, fig. 19). This tooth is again similar in overall morphology to the M2 in SDSNH 55150 but differs from the latter in having a complete cingulum below the lingual base of the protocone, an accessory cuspule on this cingulum, and a uniformly convex lingual occlusal outline. Linear dimensions of the M2 in SDSNH 55150 are 5% to 11% larger than those in the M2 of YPM-PU 10084 (West, 1984: table 8).

West (1984:47) implied that no M3s of *H. lentus* are known. However, other species of *Helohyus* have M3s that are very different from the M3 in SDSNH 55150 in that they lack a distinct posterior elongation and are similar in occlusal outline to M2; i.e., their transverse widths exceed their anteroposterior lengths (Sinclair, 1914: figs. 14–15; West, 1984: fig. 18B). Furthermore, the mean ratio of AP length to trigonid width for three m3s of *H. lentus* is 1.68, which is virtually identical to the ratio of 1.67 obtained for a large sample of m3s of *H. plicodon* (West, 1984, tables 6 and 8). On the basis of this evidence, it may be predicted that the currently unknown M3 of *H. lentus* will not be significantly elongated and so will be unlike the M3 in SDSNH 55150.

Snyder (1993) discussed two specimens of an unnamed new helohyid genus from early Uintan strata of the Sand Wash Basin, Colorado. The new genus was separated from *Parahyus* by having four rather than three lower premolars, having more complex lower premolars, and having these premolars separated by diastemata (see also Stucky, 1998:370). Associated with the lower jaws of DMNH 1764 are several skull fragments, including a left maxillary fragment with heavily damaged M2-3 (part of DMNH 2925). The M2 in DMNH 2925 is similar to the M2 in SDSNH 55150 in having finely crenulated enamel and a weak cingulum around the labial base of the metacone. However, the M2 in DMNH 2925 differs from the M2 in SDSNH 55150 in having a slightly stronger transcrista connecting the paracone and metacone, a slightly stronger rib on the posterior flank of the metacone, and a uniformly convex (rather than slightly embayed) lingual margin. The M3 in DMNH 2925 is almost completely broken away, but enough of the base of the crown remains to show that this tooth was not significantly anteroposteriorly elongated, unlike the M3 in SDSNH 55150. Consistent with this observation is the ratio of anteroposterior length to trigonid width (1.69) of the intact m3 in DMNH 1764. This value is almost identical to that noted above for *Helohyus lentus* and is much less than that for the m3 in *Parahyus vagus* (see below). Finally, the M2-3 in SDSNH 55150 range from 19% to 36% larger in linear dimensions than the M2-3 in DMNH 2925. Given the above differences, SDSNH 55150 is probably generically distinct from DMNH 1764 and 2925. The M2 in DMNH 2925 is more similar to the M2 of *Helohyus lentus* in size and general morphology (Figure 12B), but the latter tooth has a deeper ectoflexus.

The M2 in SDSNH 55150 resembles BCHS 516, the holotype M1 or 2 of *Buxobune daubreei* from the Lutetian (middle Eocene) of

Bouxwiller, France, in its essentially square occlusal outline, distinct lingual and labial cingula, and conical cusps (Sudre, 1978: plate 1, fig. 2; Sudre et al., 1983: fig. 15h). The M2 in SDSNH 55150 differs from BCHS 516 in that the latter tooth has a weaker paracone, a stronger ectocingulum, and stronger ribs on the anterior and posterior flanks of the paracone and metacone. BCHS 516 also has linear dimensions that are only about 42% of those of the M2 in SDSNH 55150. The Bouxwiller tooth is perhaps more similar in overall morphology to the M2 of *Helohyus lentus* and the M2 in DMNH 2925 but is distinctly smaller than these teeth as well.

The teeth in SDSNH 55150 are similar in size and general morphology to those of *Choeopotamus* from the middle and late Eocene of Europe (e.g., Viret, 1961: fig. 11) but differ from this genus in having much weaker cingula, in lacking a mesostyle on M2, in having an anteroposteriorly elongate rather than anteroposteriorly compressed M3, and in having fewer accessory cusps on M3.

The M2-3 in SDSNH 55150 are grossly similar in size and general morphology to the homologous teeth of the Duchesnean-Chadronian entelodont *Brachyhyops* Colbert, 1938. The M2-3 in the type skull of the small Duchesnean species *B. wyomingensis* are extremely worn (Colbert, 1938:94; Scott, 1945:245). However, two maxillary fragments (CM 11989 and 12079) referred to *B. wyomingensis* by Wilson (1971: fig. 2) show that the M2 of this species is more quadrate, has a much stronger cingulum that extends all the way around the crown, and has a much weaker hypocone than the M2 in SDSNH 55150. The M3s in CM 11989 and 12079 lack a hypocone, have a stronger circumcoronal cingulum, and are also anteroposteriorly compressed, in contrast to the hypocone-bearing, anteroposteriorly elongated M3 in SDSNH 55150. The M2-3 of the Chadronian species *B. viensis* are similar in morphology to those of *B. wyomingensis* but significantly larger (see description of SMNH P1251.1 by Storer, 1984b). The possibility that SDSNH 55150 represents an early entelodont cannot be completely dismissed, and this would seem to be plausible given Effinger's (1998: fig. 24.4) indicated Uintan temporal occurrence of *Brachyhyops*. However, the age of this alleged Uintan record is unsubstantiated. The locality in question is SB 26B (Mariano Mesa; Baca Formation, New Mexico), which is probably of Duchesnean age (Lucas, 1992:99). Stratigraphic control is lacking in the Baca Formation, and some fossil localities are apparently Uintan, while others are apparently Duchesnean (Lucas and Williamson, 1993:146).

Despite the fact that upper teeth of the large early Uintan(?) helohyid *Parahyus vagus* are unknown, SDSNH 55150 seems to be more similar to this species than to any of the other taxa discussed above. In particular, the anteroposteriorly elongated m3 in the type specimen of *Parahyus vagus* (YPM-PU 10972; AP/WTRI = 2.05; see Peterson, 1919, fig. 12; Gazin, 1955:43) suggests that M3 in this species was also anteroposteriorly elongated, probably more so than in most specimens of *Achaenodon*. Note, however, that the m3 in YPM 19817 is also somewhat elongated anteroposteriorly (AP/WTRI = 1.84). This large lower jaw from the early Uintan Tepee Trail Formation of Wyoming was identified as *Parahyus vagus* by Lewis (1973) and re-identified as *Achaenodon* sp. by McKenna (1980:339).

To estimate the size of the unknown lower teeth of the species represented by SDSNH 55150, note that in the associated skull and jaws of the type specimen of *Achaenodon robustus*, the AP length of m2 is about 98% of the AP length of M2 (Gazin, 1955:40). By applying the same proportions to the M2 in SDSNH 55150, it can be predicted that the m2 in this individual would have an AP length of 16.0 mm. This figure is in turn about 76% of the AP length (21.1 mm) of the m2 in the type specimen of *Parahyus vagus* as measured by Gazin (1955:43). *P. vagus* was noted by Gazin (1955) to be intermediate in size between the late Bridgerian *Helohyus lentus* and the early Uintan *Achaenodon*. SDSNH 55150 in turn appears to be intermediate in

size between *Helohyus lentus* and *Parahyus vagus* and may well represent a new species of the latter genus, although additional material is required to corroborate this suggestion.

As discussed by Gazin (1955:42-43), the type specimen of *Parahyus vagus* was probably collected from the Washakie Formation of Wyoming, but its exact stratigraphic provenance and age are unknown (see also Stucky, 1998:370). The only other previously reported specimen of *Parahyus* is a p3 from the early Uintan of Texas assigned to *P. vagus* by (West 1982:15). TMM 42287-15 is from the basal Tertiary conglomerate of the Devil's Graveyard Formation (Wilson, 1986:371).

Note that SDSNH Loc. 3893 occurred relatively low in the lower tongue of the Friars Formation, in association with a micromammal assemblage typical of the early Uintan Poway fauna. Although no other ungulate taxa characteristic of the Uintan were collected from SDSNH Loc. 3893 (e.g., *Amynodon*, *Leptoreodon*, *Protoreodon*, *Achaenodon*), the site was primarily a microvertebrate locality, and the largest-bodied taxon represented is *Parahyus* sp. Because the relative ages of the type locality of *P. vagus*, TMM 42287, and SDSNH Loc. 3893 are unclear, the OKR and YKR of this genus cannot be even tentatively identified. Thus, the parachron of *Parahyus* is indeterminate.

DISCUSSION

Figure 13 summarizes the known lithostratigraphic and estimated temporal ranges in San Diego County of the bunodont artiodactyls described above. Most taxa are known from only one or two localities (short vertical bars), although *Antiacodon venustus* and *Achaenodon* sp. cf. *A. robustus* are documented from several localities in the conglomerate tongue and upper tongue of the Friars Formation. No bunodont artiodactyls are known from member B of the Santiago Formation.

In addition to the taxa described here, Walsh (1996:86) listed a record of "cf. *Lophiohyus* sp." from the Friars Formation. The specimen in question is SDSNH 3612/47877, which includes left and right dentary fragments with well-worn cheek teeth and partial anterior dentitions, a well-worn M3, and associated limb and tarsal bones. Walsh (1996) tentatively identified this specimen on the basis of its possession of large diastemata between p1-2 and p2-3, which are similar to those in the type specimen of *Lophiohyus alticeps* (AMNH 1518; see Sinclair, 1914, figs. 9-10). Although McKenna and Bell (1997) retained *Lophiohyus* as a distinct genus, R. K. Stucky (pers. comm., 1997; see also Stucky, 1998) notes that the presence and magnitude of these diastemata are highly variable in species of *Helohyus* from the Bridger Formation, and that *Lophiohyus* is definitely a junior synonym of *Helohyus*. Coombs and Coombs (1977a) and West (1984) had previously reached the same conclusion. Further consideration of SDSNH 47877 suggests that it is best regarded as an oromerycid, possibly related to *Camelodon* Granger, 1910, and perhaps even referable to *Merycobunodon* Golz, 1976. I plan to describe this taxon in a revision of some of the oromerycid artiodactyls of the southern California Uintan.

PALEOENVIRONMENT

Black (1978:228) and Storer (1984a:144) tabulated the number of bunodont and selendodont artiodactyl genera and species from several Uintan assemblages of North America to infer the relative importance of forest vs. savanna type vegetation in the depositional area under consideration. The present report, with other papers published since 1984, necessitates a revision of these tabulations. Table 5 shows the number of dentally bunodont, bunosenodont, and selendodont forms from several assemblages of early and late Uintan age in western North America. Antiacodontines, leptocoerines, and

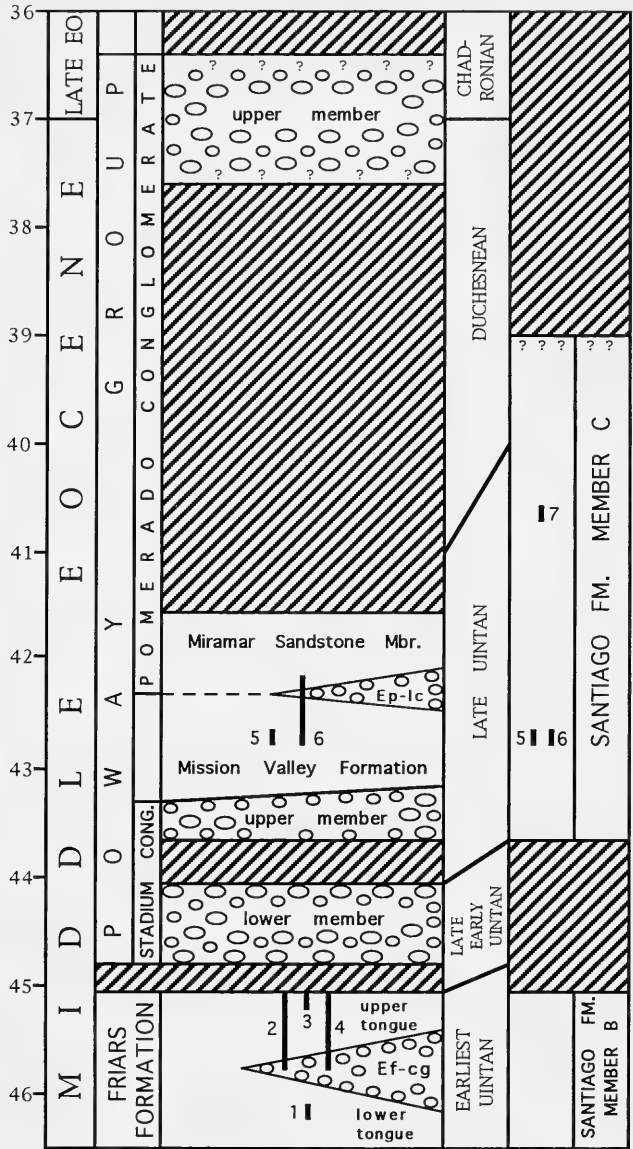


Figure 13. Known lithostratigraphic and estimated temporal ranges in San Diego County of the bunodont artiodactyl taxa discussed herein: (1), *Parahyus* sp.; (2), *Antiacodon venustus*; (3), Antiacodontinae, unident. gen. and sp.; (4), *Achaenodon* sp. cf. *A. robustus*; (5), *Ibarus* sp. nov.; (6), *Tapochoerus mcmillini*; (7), *Tapochoerus egressus*. The Friars Formation and Poway Group occur in southwestern San Diego County, while the Santiago Formation occurs in northwestern San Diego County. See Wilson (1972) and Rasmussen et al. (1995) for discussion of members B and C of the Santiago Formation. Estimated numerical ages of these units are based on information in Walsh (1996), Walsh et al. (1996), and Walsh and Gutzler (1999).

TABLE 5. Numbers of dentally bunodont, bunoselenodont, and selenodont artiodactyl genera and species in selected early and late Uintan assemblages of North America.

Assemblage	Bunodont gen./sp.	Bunoselenodont gen./sp.	Selenodont gen./sp.	Source
LATE UINTAN				
Santiago Fm., mbr. C, CA	2/3	0/0	5/9	Golz (1976); Walsh (1996; this paper). Includes the Laguna Riviera local fauna, which may be early Duchesnean in age (Walsh, 1996).
Tapo Cyn. and Brea Cyn. local faunas, CA	1/1	0/0	4/8	Kelly (1990); Kelly and Whistler (1994).
Uinta C, UT	1/1	4/5	7/12	Prothero (1996).
Badwater Locs. 5, 6, and 7, WY	2/2	0/0	6/6	Black (1978); Stucky (1998).
Candelaria local fauna, TX	0/0	0/0	3/4	Wilson (1984; 1986); Runkel (1988).
Serendipity local fauna, TX	0/0	1/1	5/7	Wilson (1984; 1986); Runkel (1988).
Casa Blanca local fauna, TX	1/1	0/0	3/4	Westgate (1990).
Swift Current Creek local fauna, SASK.	2/2	1/1	3/3	Storer (1984a; 1996).
EARLY UINTAN				
Friars Fm., CA	4-5/4-5	0/0	4/5	Golz (1976); Golz and Lillegraven (1977); Walsh (1996; this paper).
Uinta B1 + B2, UT	1/2	3/4	6/8	Prothero (1996).
Middle unit of Washakie Fm., WY	2/3	1/1	1/1	McCarroll et al. (1996).
Sand Wash Basin, CO	1/1	2/2	2/2	Stucky et al. (1996); Stucky (1998).
Whistler Squat local fauna, TX	2/2	0/0	2/4	Wilson (1984; 1986); Runkel (1988); Stucky (1998).

helohyines are considered to be bunodont forms; "homacodontines" are considered to be bunoselenodont forms; and agriocherids, oromyricids, protoceratids, hypertragulids, and camelids are considered to be selenodont forms.

As seen in Table 5, the Friars Formation contains more bunodont forms than any other early Uintan assemblage, and contains subequal numbers of bunodont and selenodont forms, but no bunoselenodont forms. The artiodactyl composition of the Whistler Squat local fauna is similar in this respect to that of the Friars Formation, but the overall diversity of Whistler Squat is lower. In general, early Uintan assemblages have subequal numbers of bunodont and bunoselenodont forms. In contrast, late Uintan assemblages generally have slightly fewer bunodont forms and a greater number of selenodont forms, as expected from the observations of Black (1978) and Storer (1984a). The large number of bunoselenodont forms known from the Uinta Formation may be attributable to significant time-averaging, which would result in a greater diversity of taxa than was present in this area at any one time.

Given the relatively high proportions of bunodont taxa in the Swift Current Creek local fauna, Storer (1984a) suggested that this fossil assemblage accumulated in a local setting less savanna-like than the paleoenvironments prevailing during the deposition of coeval Uintan assemblages in the Rocky Mountains, west Texas, and southern California. However, the data summarized in Table 5 now indicate that the diversity of bunodont forms in the Swift Current Creek local fauna was similar to that in other late Uintan assemblages (e.g., member C of the Santiago Formation and Badwater localities 5, 6, and 7).

Stucky (1985:275–276) urged caution in using proportions of bunodont and selenodont forms to infer paleoenvironment. Leaf fossils from the Friars and Mission Valley formations exist in UCMP and SDSNH collections (Lillegraven, 1979; Walsh, 1996) but have not been formally studied. Fortunately, recent palynological work on the San Diego Eocene allows us to attack the problem better. Frederiksen (1989; 1991) documented a pollen assemblage from the late Uintan Mission Valley Formation. Frederiksen (1991:568) stated:

This flora includes a high diversity of pollen types probably produced by trees (for example, Palmae, Bombacaceae-Sterculiaceae-Tiliaceae complex, Eucommiaceae, Faga-

ceae(?), Juglandaceae, Myrtaceae(?), Symplocaceae(?), Ulmaceae); many additional pollen taxa most likely produced by shrubs or trees; and a scarcity of pollen taxa obviously produced by herbs.

Frederiksen (1991) noted that it was "difficult to determine on the basis of the pollen flora whether narrow gallery forests existed [on the San Diego coastal plain during Mission Valley time] . . . or whether the savanna was 'traversed by streams whose floodplains supported a relatively luxuriant mesic forest of many species' (MacGinitie, 1969, p. 49)." Nevertheless, Frederiksen (1991:568) noted that relatively little pollen/spore turnover occurred between Bridgerian and late Uintan time in San Diego, as evidenced by microfossils from the Delmar Formation and Ardath Shale compared to the microflora from the Mission Valley Formation. As the early middle Eocene (probably Bridgerian) Torrey flora indicates a warm, paratropical climate for San Diego (Myers, 1991), the late Uintan climate and paleoenvironment was probably similar.

Frederiksen (1991) also recognized a "Middle Eocene Diversity Decline" (MEDD) in pollen assemblages that took place in southern California and the Gulf Coast beginning in the late middle Eocene. Recognition of this event in California was based on pollen assemblages from middle Eocene strata of the San Diego area and middle to late Eocene strata of the Transverse Ranges (Frederiksen, 1989). The MEDD was estimated by Frederiksen (1991, fig. 3) to have begun during the early Bartonian (42–43 Ma using the time scale of Berggren et al., 1985, but 40–41 Ma using the time scale of Berggren et al., 1995). The MEDD, therefore, probably began during the early Duchesnean, soon after deposition of the pre-MEDD, late Uintan Mission Valley Formation. According to Frederiksen (1991), the MEDD reflected a major climatic cooling and drying event that affected southern California and the Gulf Coast in different ways. The general later Eocene climatic deterioration in North America has also been discussed by Leopold et al. (1992). Frederiksen (1991:568) stated:

In the Gulf Coast . . . the MEDD was immediately followed by a burst of first appearances of angiosperm taxa including many shrubs and herbs, among them the first grasses (Gramineae). However, in southern California, the MEDD was not followed by significant first appearances of taxa; that is why

there is no indication of an increase in angiosperm pollen diversity in the middle Bartonian in southern California as there was on the Gulf Coast . . . No pollen definitely of Gramineae has been found in the Eocene of southern California.

Despite the apparent lack of grasses in the Uintan environment of southern California, a healthy diversity of selenodont artiodactyls thrived in this province (Golz, 1976). As noted by Gregory (1971:69), however, this should not be surprising, because the teeth of these relatively low-crowned Uintan selenodonts "are more comparable to those of [modern] browsing deer and chevrotain than to any grazers" (see Webb, 1977:362).

Although the climate change that apparently caused the early Duchesnean MEDD cannot be invoked as a causal mechanism to explain the early Uintan-late Uintan mammalian faunal turnover in southern California (Walsh, 1996), it has obvious implications for the evolution of North American mammalian faunas during the Duchesnean, and the establishment of the Chadronian-Whitneyan White River Chronofauna (Tedford et al., 1987). In this fauna, the only remaining bunodont artiodactyls indigenous to North America were the leptochoerids, which were never diverse or numerically abundant (Edwards, 1976).

PALEOBIOGEOGRAPHY

Golz (1976) examined the paleobiogeographic distribution of Eocene artiodactyl taxa between the western interior and California

and noted that only one bunodont taxon (*Tapochoerus egressus*) was then known from the latter region. The specimens described here show that while the California Uintan faunas contained several bunodont taxa, they were still depauperate relative to those of the western interior. Table 6 summarizes the currently known geographic distribution of middle Eocene bunodont and bunoselenodont genera in California, the Rocky Mountains, Texas, and Saskatchewan.

The presence of *Antiacodon venustus* in the early Uintan of San Diego constitutes another species-level taxonomic similarity between the early Uintan fauna of San Diego and the late Bridgerian fauna of the Rocky Mountains (Lillegraven, 1979; Walsh, 1996). The genus *Antiacodon* has yet to be confidently recorded from any other early Uintan assemblage in North America. Conversely, the antiacodontine *Auxontodon* is known from the late Uintan of Utah and Wyoming (Gazin, 1958; Storer, 1984a; Stucky, 1998), the late Uintan of Saskatchewan (Storer, 1984a), possibly the late Uintan of trans-Pecos Texas (Stucky, 1998:365), possibly the early Uintan of Wyoming (Eaton, 1985), and possibly the Duchesnean of British Columbia (Stucky, 1998:365), but has not been recorded from California.

Yet to be collected from the early Uintan of San Diego are the characteristic Bridger Formation taxa *Microsus*, *Helohyus*, and *Homacodon*. West (1982) reported all three of these genera from the early Uintan of Texas (Whistler Squat local fauna), but Stucky (1998:367) concluded that the alleged *Microsus* tooth (TMM 41372-245; West, 1982: fig. 6B) pertains to *Hylomeryx* sp. In addition, TMM 41443-470 (the m1 or 2 identified by West, 1982: fig. 6C as *Helohyus* sp.) is clearly a macrotarsine primate. Stucky (1998:367) recognized

TABLE 6. Geographic distribution of middle Eocene bunodont and bunoselenodont genera in four provincial areas of western North America. Compiled from West (1982), Wilson (1986), Storer (1984a), Runkel (1988), Stucky (1998), and this paper.

	California	Rocky Mtns.	Texas	Saskatchewan
Duchesnean	—	<i>Brachyhyops</i>	<i>Brachyhyops</i>	—
	—	<i>Pentacemylus</i>	—	—
		leptochoerid, gen. nov.	—	—
	—	—	<i>Texodon</i>	—
	—	<i>Apriculus</i>	—	—
	—	<i>Pentacemylus</i>	—	—
	—	<i>Mytonomeryx</i>	—	—
	—	<i>Mesomeryx</i>	—	—
Late Uintan	—	<i>Bunomeryx</i>	—	—
	—	<i>Hylomeryx</i>	—	—
	—	<i>Auxontodon</i>	<i>Auxontodon?</i>	<i>Auxontodon</i>
	<i>Tapochoerus</i>	—	—	—
	<i>Ibarus</i>	—	—	<i>Ibarus</i>
	—	—	<i>Laredochoerus</i>	—
	—	—	<i>Texodon</i>	—
	—	<i>Bunomeryx</i>	—	—
	—	<i>Mesomeryx</i>	—	—
	—	<i>Hylomeryx</i>	<i>Hylomeryx</i>	—
Early Uintan	<i>Achaenodon</i>	<i>Achaenodon</i>	—	—
	<i>Parahyus</i>	<i>Parahyus</i>	<i>Parahyus</i>	—
	—	helohyid, gen. nov.	—	—
	—	—	<i>Helohyus</i>	—
	<i>Antiacodon</i>	—	—	—
	—	—	"D." woltonensis	—
	—	<i>Antiacodon</i>	—	—
	—	<i>Neodiacodexis</i>	—	—
Later Bridgerian	—	"D." woltonensis	—	—
	—	<i>Microsus</i>	—	—
	—	<i>Homacodon</i>	—	—
	—	<i>Helohyus</i>	—	—

this fact, but inadvertently implied that the tooth in question was TMM 41443-531, which is undoubtedly an m3 (West, 1982: fig. 6D). Nevertheless, *Helohyus lentus* was recorded from the late Bridgerian or early Uintan part of the Canoe Formation of Texas by Wilson (1967) and Runkel (1988), and West's (1982) record of *Lophiohyus* sp. from the Whistler Squat local fauna was referred to *H. milleri* by Stucky (1998:369). Finally, West's (1982: fig. 6D) assignment of TMM 41443-531 to *Homacodon* cf. *H. vagans* is questionable (note the extremely small hypoconulid lobe), and indeed Stucky (1998:367) did not list *Homacodon* from Locality SB43A (Whistler Squat local fauna). As a result of these revised identifications, the Whistler Squat local fauna contains fewer "Bridgerian holdover taxa" than previously supposed.

Achaenodon is known from the early Uintan of San Diego and the Rocky Mountains but has yet to be recorded from the early Uintan of Texas. However, fossils of this genus are sufficiently uncommon that its apparent absence in the latter region may still be ascribed to collecting bias (early Uintan rocks are unknown in Saskatchewan). Note that the middle Bridgerian to early Uintan temporal range of *Achaenodon* shown by Stucky (1998: fig. 23.6) is a drafting error (Stucky, pers. comm.). This genus is known only from the early Uintan. *Parahyus* is now known from the early Uintan of San Diego, Wyoming, and Texas.

Walsh's (1996, table 2) record of *Ibarus* sp. cf. *I. ignotus* from late Uintan localities in San Diego constitutes the first record of the Leptochoerinae from the California Eocene. *Ibarus* was previously known only from the late Uintan of Saskatchewan (Storer, 1984a), and the San Diego specimens pertain to a new species of the genus (Walsh, ms). According to R. K. Stucky (pers. comm.), the San Diego specimens are also similar to those of "*Diacodexys*" *woltonensis*, which was recorded by Stucky (1998:363) from both the Bridger Formation and the early Uintan Whistler Squat local fauna of trans-Pecos Texas. The late Uintan leptochoerid from Texas (*Laredochoerus*) is markedly different from *Ibarus* (see Westgate, 1994), and the poorly known early Duchesnean leptochoerid from Badwater, Wyoming, is also distinct (Black, 1978; Stucky, 1998:364). Storer (1996:248) also recorded an indeterminate leptochoerid from the Duchesnean Lac Pelletier Lower Fauna of Saskatchewan.

Still unknown from the Uintan rocks of California are several "homacodont" taxa common in the Uinta Formation, i.e., *Mesomeryx*, *Bunomeryx*, *Hylomeryx*, *Mytonomeryx*, and *Pentacemylus*. Their absence in California may be real rather than merely apparent, because collecting bias can now be ruled out with more confidence than was possible at the time of Golz's (1976) study. Why these taxa should have failed to disperse to the West Coast at some time during the Uintan is mysterious, as several species of *Protoreodon*, *Leptoreodon*, and *Protylopus* had no trouble doing so. Golz's (1976:24) suggestion that the numerous California species of the latter genera "offered too much competition to any possible invasion by other selenodont genera or by homacodontine dichobunids" remains possible. An alternative explanation would be that the homacodontines of the western interior were adapted to vegetational types that did not exist in southern California. Unfortunately, Uintan megaflores and palynological assemblages of the Rocky Mountains are poorly known. MacGinitie (1974:64-65) briefly described floral assemblages from Uintan strata of the Tepee Trail and Washakie formations of Wyoming and noted the presence (although not the abundance) of Gramineae in the Uintan part of the Washakie Formation. Given the absence of grasses in the Uintan of California (Fredericksen, 1991), this may constitute a hint of vegetational differences between the two areas that could control the distribution of artiodactyl taxa.

The poorly represented genus *Texodon* is known only from the Uintan of Texas (West, 1982; Runkel, 1988; Stucky, 1998), and the poorly represented genus *Apriculus* is known only from the late Uintan of Badwater, Wyoming (Gazin, 1956; Coombs and Coombs,

1977b; Stucky, 1998).

Duchesnean faunas are relatively sparse, and the only known bunodont and bunoselenodont taxa of this age are the unnamed leptochoerid genus from Wyoming (Black, 1978; Stucky, 1998:364), the indeterminate leptochoerid from Saskatchewan noted by Storer (1996), *Pentacemylus* (a late Uintan holdover), and *Brachyhyops*, the oldest known North American entelodont (e.g., Wilson, 1971). Emry (1981:568) and McKenna and Bell (1997:412) regarded *Dyscritochoerus* Gazin, 1956, as a junior synonymy of *Brachyhyops*, but Stucky (1998:370) agreed with Gazin that the type and only known specimen (CM 11912; originally described as *Helohyus*?) sp. by Peterson, 1934) represented a distinct genus. Unfortunately, this specimen has apparently been lost for at least 44 years (Gazin, 1956:26; Stucky, 1998:370), so the potential synonymy of *Dyscritochoerus* and *Brachyhyops*, while reasonable, is inconclusive (Wilson, 1971:12). The latter name is used in Table 6 for simplicity.

ACKNOWLEDGMENTS

I thank S. E. Foss, J. A. Lillegraven, S. G. Lucas, M. C. McKenna, R. K. Stucky, and J. Sudre for discussions and information; J. D. Archibald for access to a measuring microscope; and T. A. Deméré, J. E. Storer, and R. K. Stucky for reviewing the manuscript. Important San Diego County specimens were collected by G. Calvano, R. A. Cerutti, R. L. Clark, B. O. Riney, and P. J. Sena, and skillfully prepared by Cerutti, Clark, and Riney. I thank J. P. Alexander (AMNH), H. N. Bryant (SMNH), M. Cassiliano (UW), R. J. Emry and R. Purdy (USNM), P. Holroyd (UCMP), P. Mayer (MPM), A. Tabrum (CM), S. A. McLeod (LACM), P. Murphy (UCM), C. R. Schaff (MCZ), R. K. Stucky (DMNH), and M. A. Turner (YPM) for loans of specimens and/or casts. Collection and curation of the San Diego County fossils described herein was made possible by the California Department of Transportation, Gatlin Development, D. R. Horton, McMillin Communities, Monarch Communities of California, and Shea Homes.

LITERATURE CITED

- Berggren, W. A., D. V. Kent, J. J. Flynn, and J. A. Van Couvering. 1985. Cenozoic geochronology. Geological Society of America Bulletin 96:1407-1418.
- Berggren, W. A., D. V. Kent, C. C. Swisher III, and M.-P. Aubry. 1995. A revised Cenozoic geochronology and chronostratigraphy, pp. 129-212 in W. A. Berggren, D. V. Kent, and J. Hardenbol (eds.), Geochronology, Time Scales and Global Stratigraphic Correlations: A Unified Temporal Framework for an Historical Geology. Society of Economic Paleontologists and Mineralogists, Special Publication 54.
- Black, C. C. 1978. Paleontology and geology of the Badwater Creek area, central Wyoming. Part 14. The artiodactyls. Annals of Carnegie Museum 47:223-259.
- Burke, J. J. 1969. An antiodont from the Green River Eocene of Utah. Kirtlandia 5:1-7.
- Colbert, E. H. 1938. *Brachyhyops*, a new bunodont artiodactyl from Beaver Divide, Wyoming. Annals of Carnegie Museum 27:87-108.
- Coombs, M. C., and W. P. Coombs. 1977a. Dentition of *Gobiohyus* and a reevaluation of the Helohyidae (Artiodactyla). Journal of Mammalogy 58:291-308.
- Coombs, M. C., and W. P. Coombs. 1977b. The origin of anthracotheres. Neues Jahrbuch fuer Geologie und Palaeontologie, Abhandlungen 10:584-599.
- Cope, E. D. 1872. Description of some new Vertebrata from the Bridger group of the Eocene. Proceedings of the American Philosophical Society 12:460-465.
- Cope, E. D. 1873a. On some Eocene mammals obtained by Hayden's Geological Survey of 1872. Palaeontological Bulletin 12:1-6.
- Cope, E. D. 1873b. Fourth notice of extinct Vertebrata from the Bridger and the Green River Tertiaries. Palaeontological Bulletin 17:1-4.
- Cope, E. D. 1875. On fossil lemurs and dogs. Proceedings of the Acad-

- omy of Natural Sciences of Philadelphia, (no volume number for 1875), pp. 255–256.
- Cope, E. D. 1884. The Vertebrata of the Tertiary Formations of the West, Book I; pp. 1–1009 in F. V. Hayden (geologist-in-charge), Report of the U. S. Geological Survey of the Territories, Volume III. Government Printing Office, Washington, D. C.
- Eaton, J. G. 1985. Paleontology and correlation of the Eocene Tepee Trail and Wiggins formations in the North Fork of Owl Creek area, southeastern Absaroka Range, Hot Springs County, Wyoming. *Journal of Vertebrate Paleontology* 5:345–370.
- Edwards, P. 1976. The subfamily Leptochoerinae (Artiodactyla, Dichobunidae) of North America (Oligocene). University of Wyoming Contributions to Geology 14:99–113.
- Effinger, J. A. 1998. Entelodontidae; pp. 375–380 in C. M. Janis, K. M. Scott, and L. L. Jacobs (eds.), *Evolution of Tertiary Mammals of North America*. Cambridge University Press, Cambridge, England.
- Emry, R. J. 1981. Additions to the mammalian fauna of the type Duchesnean, with comments on the status of the Duchesnean "Age." *Journal of Paleontology* 55:563–570.
- Emry, R. J. 1990. Mammals of the Bridgerian (middle Eocene) Elderberry Canyon local fauna of eastern Nevada; pp. 187–210 in T. M. Bown and K. D. Rose (eds.), *Dawn of the Age of Mammals in the northern part of the Rocky Mountain Interior, North America*. Geological Society of America Special Paper 243.
- Franzen, J. L. 1981. Das erste Skelett eines Dichobuniden (Mammalia, Artiodactyla), geborgen aus mitteleozänen Olschiefern der "Grube Messel" bei Darmstadt (Deutschland, S-Hessen). *Senckenbergiana Lethaia* 61:299–353.
- Franzen, J. L. 1983. Ein zweites Skelett von *Messelobunodon* (Mammalia, Artiodactyla, Dichobunidae) aus der "Grube Messel" bei Darmstadt (Deutschland, S-Hessen). *Senckenbergiana Lethaia* 64:403–445.
- Frederiksen, N. O. 1989. Eocene spormorph biostratigraphy of southern California. *Palaentographica*, Abteilung B, 211:135–179.
- Frederiksen, N. O. 1991. Pulses of middle Eocene to earliest Oligocene climatic deterioration in southern California and the Gulf Coast. *Palaios* 6:564–571.
- Gazin, C. L. 1952. The lower Eocene Knight Formation of western Wyoming and its mammalian faunas. *Smithsonian Miscellaneous Collections* 117 (18):1–82.
- Gazin, C. L. 1955. A review of the upper Eocene Artiodactyla of North America. *Smithsonian Miscellaneous Collections* 128 (8):1–96.
- Gazin, C. L. 1956. The geology and vertebrate paleontology of upper Eocene strata in the northeastern part of the Wind River Basin, Wyoming. Part 2. The mammalian fauna of the Badwater area. *Smithsonian Miscellaneous Collections* 131 (8):1–35.
- Gazin, C. L. 1958. A new dichobunid artiodactyl from the Uinta Eocene. *Breviora* 96:1–6.
- Gazin, C. L. 1962. A further study of the lower Eocene mammalian faunas of southwestern Wyoming. *Smithsonian Miscellaneous Collections* 144 (1):1–98.
- Gazin, C. L. 1976. Mammalian faunal zones of the Bridger middle Eocene. *Smithsonian Contributions to Paleobiology* 26:1–25.
- Gentry, A. W., and J. J. Hooker. 1988. The phylogeny of the Artiodactyla; pp. 235–272 in M. J. Benton (ed.), *The Phylogeny and Classification of the Tetrapods, Volume 2: Mammals*. Clarendon Press, Oxford, England.
- Golz, D. J. 1976. Eocene Artiodactyla of southern California. *Los Angeles County Natural History Museum Bulletin* 26:1–85.
- Golz, D. J., and J. A. Lillegraven. 1977. Summary of known occurrences of terrestrial vertebrates from Eocene strata of southern California. *Contributions to Geology*, University of Wyoming 15:43–65.
- Granger, W. 1910. Tertiary faunal horizons in the Wind River Basin, Wyoming, with descriptions of new Eocene mammals. *American Museum of Natural History Bulletin* 28:235–251.
- Gregory, J. T. 1971. Speculations on the significance of fossil vertebrates for the antiquity of the Great Plains of North America. *Abhandlungen des Hessisches Landesamtes fuer Bodenforschung (Heinz Tobien Festschrift)* 60:64–72.
- Gunnell, G. F. 1998. Mammalian fauna from the lower Bridger Formation (Bridger A, early middle Eocene) of the southern Green River Basin, Wyoming. *Contributions from the Museum of Paleontology, University of Michigan* 30:83–130.
- Guthrie, D. A. 1971. The mammalian fauna of the Lost Cabin Member, Wind River Formation (Lower Eocene) of Wyoming. *Annals of Carnegie Museum* 43:47–113.
- Holroyd, P. A., and R. L. Ciochon. 1995. A new artiodactyl (Mammalia) from the Eocene Pondaung sandstones, Burma. *Annals of Carnegie Museum* 64:177–183.
- Kelly, T. S. 1990. Biostratigraphy of the Uintan and Duchesnean land mammal assemblages from the middle member of the Sespe Formation, Simi Valley, California. *Los Angeles County Natural History Museum Contributions in Science* 419:1–42.
- Kelly, T. S., E. B. Lander, D. P. Whistler, M. A. Roeder, and R. E. Reynolds. 1991. Preliminary report on a paleontologic investigation of the lower and middle members, Sespe Formation, Simi Valley Landfill, Ventura County, California. *Paleobios* 13 (50):1–13.
- Kelly, T. S., and D. P. Whistler. 1994. Additional Uintan and Duchesnean (middle and late Eocene) mammals from the Sespe Formation, Simi Valley, California. *Los Angeles County Natural History Museum Contributions in Science* 439:1–29.
- Kennedy, M. P. 1975. Geology of the San Diego metropolitan area, California. *California Division of Mines and Geology Bulletin* 200A:9–38.
- Kennedy, M. P., and G. L. Peterson. 1975. Geology of the San Diego metropolitan area, California. *California Division of Mines and Geology Bulletin* 200B:43–56.
- Kennedy, M. P., and G. W. Moore. 1971. Stratigraphic relations of Upper Cretaceous and Eocene formations, San Diego coastal region, California. *American Association of Petroleum Geologists Bulletin* 55:709–722.
- Krishtalka, L., and R. K. Stucky. 1985. Revision of the Wind River Faunas, early Eocene of central Wyoming. Part 7. Revision of *Diacodexis* (Mammalia, Artiodactyla). *Annals of Carnegie Museum* 54:413–486.
- Krishtalka, L., and R. K. Stucky. 1986. Early Eocene artiodactyls from the San Juan Basin, New Mexico, and the Piceance Basin, Colorado. *Contributions to Geology, University of Wyoming, Special Paper* 3:183–196.
- Leopold, E. B., G. Liu, and S. Clay-Poole. 1992. Low-biomass vegetation in the Oligocene?; pp. 399–420 in D. R. Prothero and W. A. Berggren (eds.), *Eocene–Oligocene Climatic and Biotic Evolution*. Princeton University Press, Princeton, New Jersey.
- Lewis, G. E. 1973. A second specimen of *Parahyus vagus* Marsh, 1876. *United States Geological Survey Journal of Research* 1:147–149.
- Lillegraven, J. A. 1979. A biogeographical problem involving comparisons of later Eocene terrestrial vertebrate faunas of western North America; pp. 333–47 in J. Gray and A. J. Boucot (eds.), *Historical biogeography, plate tectonics, and the changing environment*. Oregon State University Press, Corvallis.
- Lucas, S. G. 1992. Redefinition of the Duchesnean land mammal "age," late Eocene of western North America; pp. 88–105 in D. R. Prothero and W. A. Berggren (eds.), *Eocene–Oligocene Climatic and Biotic Evolution*. Princeton University Press, Princeton, New Jersey.
- Lucas, S. G., and T. E. Williamson. 1993. Eocene vertebrates and late Laramide stratigraphy of New Mexico; pp. 145–158 in S. G. Lucas and J. Zidek (eds.), *Vertebrate Paleontology in New Mexico*. New Mexico Museum of Natural History and Science Bulletin 29.
- Macdonald, J. R. 1955. The Leptochoeridae. *Journal of Paleontology* 29:439–459.
- MacGinitie, H. D. 1969. The Eocene Green River flora of northwestern Colorado and northeastern Utah. *University of California Publications in Geological Sciences* 83:1–140.
- MacGinitie, H. D. 1974. An early middle Eocene flora from the Yellowstone–Absaroka volcanic province, northwestern Wind River Basin, Wyoming. *University of California Publications in Geological Sciences* 108:1–103.
- Marsh, O. C. 1872. Preliminary description of new Tertiary mammals. Part II. *American Journal of Science, Third Series*, 4:202–224.
- Marsh, O. C. 1876. Notice of new Tertiary mammals, V. *American Journal of Science, Third Series*, 12:401–404.
- Marsh, O. C. 1877. Introduction and succession of vertebrate life in America. *American Journal of Science, Third Series*, 14:337–378.
- Marsh, O. C. 1894. Description of Tertiary artiodactyls. *American Journal of Science, Third Series*, 48:259–274.
- McCarroll, S. M., J. J. Flynn, and W. D. Turnbull. 1996. Biostratigraphy

- and magnetostratigraphy of the Bridgerian–Uintan Washakie Formation, Washakie Basin, Wyoming; pp. 25–39 in D. R. Prothero and R. J. Emry (eds.), *The Terrestrial Eocene–Oligocene Transition in North America*. Cambridge University Press, Cambridge, England.
- McKenna, M. C. 1959. *Tapochoeris*, a Uintan dichobunid artiodactyl from the Sespe Formation of California. *Bulletin of the Southern California Academy of Sciences* 58:125–132.
- McKenna, M. C. 1980. Late Cretaceous and early Tertiary vertebrate paleontological reconnaissance, Togwotee Pass area, northwestern Wyoming; pp. 321–343 in L. L. Jacobs (ed.), *Aspects of Vertebrate History*. Museum of Northern Arizona Press, Flagstaff.
- McKenna, M. C., and S. K. Bell. 1997. *Classification of Mammals above the Species Level*. Columbia University Press, New York.
- Murphey, P. C., A. Lester, B. Bohor, P. Robinson, E. Evanoff, and E. Larson. 1999. $^{40}\text{Ar}/^{39}\text{Ar}$ dating of volcanic ash deposits in the Bridger Formation (middle Eocene), southwestern Wyoming. *Geological Society of America Abstracts with Programs* 31:A-233.
- Myers, J. A. 1991. The early middle Eocene Torrey flora, Del Mar, California; pp. 201–215 in P. L. Abbott and J. A. May (eds.), *Eocene Geologic History San Diego Region*. Pacific Section SEPM Volume 68.
- Osborn, H. F. 1883. *Achaenodon*, an Eocene bunodont. Contributions from the E. M. Museum of Geology and Archaeology, Princeton College, Bulletin 3:23–35.
- Osborn, H. F. 1895. Fossil mammals of the Uinta Basin: Expedition of 1894. *American Museum of Natural History Bulletin* 7:71–105.
- Osborn, H. F. 1902. American Eocene primates, and the supposed rodent family Mixodectidae. *American Museum of Natural History Bulletin* 16:169–214.
- Peterson, O. A. 1919. A report upon the material discovered in the upper Eocene of the Uinta Basin by Earl Douglass in the years 1908–1909, and by O. A. Peterson in 1912. *Annals of Carnegie Museum* 12:40–168.
- Peterson, O. A. 1934. List of species and description of new material from the Duchesne River Oligocene, Uinta Basin, Utah. *Annals of Carnegie Museum* 23:373–389.
- Prothero, D. R. 1996. Magnetic stratigraphy and biostratigraphy of the middle Eocene Uinta Formation, Uinta Basin, Utah; pp. 3–24 in D. R. Prothero and R. J. Emry (eds.), *The Terrestrial Eocene–Oligocene Transition in North America*. Cambridge University Press, Cambridge, England.
- Prothero, D. R., J. L. Howard, and T. H. Huxley Dozier. 1996. Stratigraphy and paleomagnetism of the upper middle Eocene to lower Miocene (Uintan to Arikarean) Sespe Formation, Ventura County, California; pp. 171–188 in D. R. Prothero and R. J. Emry (eds.), *The Terrestrial Eocene–Oligocene Transition in North America*. Cambridge University Press, Cambridge, England.
- Rasmussen, D. T., M. Shekelle, S. L. Walsh, and B. O. Riney. 1995. The dentition of *Dyscolemur*, and comments on the use of the anterior teeth in primate systematics. *Journal of Human Evolution* 29:301–320.
- Robinson, P. 1966. Fossil Mammalia of the Huerfano Formation, Eocene, of Colorado. *Peabody Museum of Natural History Bulletin* 21:1–95.
- Runkel, A. C. 1988. Stratigraphy, sedimentology, and vertebrate paleontology of Eocene rocks, Big Bend region, Texas. Doctoral thesis. University of Texas at Austin.
- Russell, D. E., J. G. M. Thewissen, and D. Sigogneau-Russell. 1983. A new dichobunid artiodactyl (Mammalia) from the Eocene of north-west Pakistan. Part II. Cranial osteology. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen, Series B*, 86:285–300.
- Scott, W. B. 1940. The mammalian fauna of the White River Oligocene. Part III. Artiodactyla. *Transactions of the American Philosophical Society* 28:363–746.
- Scott, W. B. 1945. The Mammalia of the Duchesne River Oligocene. *Transactions of the American Philosophical Society* 34:209–253.
- Sinclair, W. J. 1914. A revision of the bunodont Artiodactyla of the middle and lower Eocene of North America. *American Museum of Natural History Bulletin* 33:267–295.
- Snyder, J. R. 1993. A new genus of Helohyidae (Mammalia, Artiodactyla) from the Sand Wash Basin, Colorado (Washakie Formation, Eocene, earliest Uintan). *Journal of Vertebrate Paleontology* 13, supplement to no. 3:58A (abstract).
- Stock, C. 1934a. Microsopsinae and Hyposodontidae in the Sespe upper Eocene, California. *National Academy of Sciences Proceedings* 20:349–354.
- Stock, C. 1934b. A hypertragulid from the Sespe uppermost Eocene, California. *National Academy of Sciences Proceedings* 20:625–629.
- Stock, C. 1936. *Hesperomeryx*, a new artiodactyl from the Sespe Eocene, California. *National Academy of Sciences Proceedings* 22:177–182.
- Storer, J. E. 1984a. Mammals of the Swift Current Creek Local Fauna (Eocene, Uintan, Saskatchewan). *Saskatchewan Museum of Natural History Contributions* 7:1–158.
- Storer, J. E. 1984b. Fossil mammals of the Southfork local fauna (early Chadronian) of Saskatchewan. *Canadian Journal of Earth Sciences* 21:1400–1405.
- Storer, J. E. 1996. Eocene–Oligocene faunas of the Cypress Hills Formation, Saskatchewan; pp. 240–261 in D. R. Prothero and R. J. Emry (eds.), *The Terrestrial Eocene–Oligocene Transition in North America*. Cambridge University Press, Cambridge, England.
- Stucky, R. K. 1985. Review [of Storer, 1984a]. *Journal of Vertebrate Paleontology* 5:274–277.
- Stucky, R. K. 1998. Eocene bunodont and bunoselendodont Artiodactyla (“dichobunids”); pp. 358–374 in C. M. Janis, K. M. Scott, and L. L. Jacobs (eds.), *Evolution of Tertiary Mammals of North America*. Cambridge University Press, Cambridge, England.
- Stucky, R. K., D. R. Prothero, W. G. Lohr, and J. R. Snyder. 1996. Magnetic stratigraphy, sedimentology, and mammalian faunas of the early Uintan Washakie Formation, Sand Wash Basin, northwestern Colorado; pp. 40–51 in D. R. Prothero and R. J. Emry (eds.), *The Terrestrial Eocene–Oligocene transition in North America*. Cambridge University Press, Cambridge, England.
- Sudre, J. 1978. Les artiodactyles de l’Éocène moyen et supérieur d’Europe occidentale (système et évolution). *Mémoires et Travaux de l’Institut de Montpellier* 7:1–229.
- Sudre, J., D. E. Russell, P. Louis, and D. E. Savage. 1983. Les artiodactyles de l’Éocène inférieur d’Europe (Deuxième partie). *Bulletin du Muséum National d’Histoire Naturelle, Paris, 4th series, section C*, 5:339–365.
- Tedford, R. H., M. F. Skinner, R. W. Fields, J. M. Rensberger, D. P. Whistler, T. Galusha, B. E. Taylor, J. R. Macdonald, and S. D. Webb. 1987. Faunal succession and biochronology of the Arikarean through Hemphillian interval (late Oligocene through earliest Pliocene Epochs) in North America; pp. 153–210 in M. O. Woodburne (ed.), *Cenozoic Mammals of North America: Geochronology and Biostratigraphy*. University of California Press, Berkeley.
- Theodor, J. 1999. *Protoreodon walshi*, a new species of agriocherid (Oreodontia, Artiodactyla, Mammalia) from the late Uintan of San Diego County, California. *Journal of Paleontology* 73:1179–1190.
- Thewissen, J. G. M., D. E. Russell, P. D. Gingerich, and S. T. Hussain. 1983. A new dichobunid artiodactyl (Mammalia) from the Eocene of North-West Pakistan: Dentition and Classification. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen, Series B*, 86:153–180.
- Viret, J. 1961. Artiodactyla; pp. 887–961 in J. Piveteau (ed.), *Traité de Paléontologie*, VI. Masson, Paris.
- Walsh, S. L. 1996. Middle Eocene mammal faunas of San Diego County, California; pp. 75–119 in D. R. Prothero and R. J. Emry (eds.), *The Terrestrial Eocene–Oligocene Transition in North America*. Cambridge University Press, Cambridge, England.
- Walsh, S. L. 1998. Fossil datum terms, paleobiological event terms, paleontostratigraphy, chronostratigraphy, and the definition of land-mammal “age” boundaries. *Journal of Vertebrate Paleontology* 18:150–179.
- Walsh, S. L., and R. Q. Gutzler. 1999. Late Duchesnean–early Chadronian mammals from the upper member of the Pomerado Chronolite, San Diego, California. *Journal of Vertebrate Paleontology* 19, supplement to no. 3:82A (abstract).
- Walsh, S. L., D. R. Prothero, and D. J. Lundquist. 1996. Stratigraphy and paleomagnetism of the middle Eocene Friars Formation and Poway Group in southwestern San Diego County, California; pp. 120–154 in D. R. Prothero and R. J. Emry (eds.), *The Terrestrial Eocene–Oligocene Transition in North America*. Cambridge University Press, Cambridge, England.

- Webb, S. D. 1977. A history of savanna vertebrates in the New World. Part 1. North America. *Annual Review of Ecology and Systematics* 8:355–380.
- West, R. M. 1973. Geology and mammalian paleontology of the New Fork–Big Sandy area, Sublette County, Wyoming. *Fieldiana Geology* 29:1–193.
- West, R. M. 1982. Fossil mammals from the Lower Buck Hill Group, Eocene of trans-Pecos Texas: Marsupicarnivora, Primates, Taeniodonta, Condylarthra, bunodont Artiodactyla, and Dinocerata. *Pearce-Sellards Series* 35:1–20.
- West, R. M. 1984. Paleontology and geology of the Bridger Formation, Southern Green River Basin, southwestern Wyoming. Part 7. Survey of Bridgerian Artiodactyla, including description of a skull and partial skeleton of *Antiacodon pygmaeus*. *Milwaukee Public Museum Contributions in Biology and Geology* 56:1–47.
- West, R. M., and E. G. Atkins. 1970. Additional middle Eocene (Bridgerian) mammals from Tabernacle Butte, Sublette County, Wyoming. *American Museum Novitates* 2404:1–26.
- Westgate, J. W. 1990. Uintan land mammals (excluding rodents) from an estuarine facies of the Laredo Formation (middle Eocene, Claiborne Group), Webb County, Texas. *Journal of Paleontology* 64: 454–468.
- Westgate, J. W. 1994. A new leptocoerid from middle Eocene (Uintan) deposits of the Texas Coastal Plain. *Journal of Vertebrate Paleontology* 14: 296–299.
- Wilson, J. A. 1967. Early Tertiary mammals; pp. 157–169 in R. A. Maxwell, J. T. Lonsdale, R. T. Hazzard, and J. A. Wilson, *Geology of Big Bend National Park*. University of Texas Publication 6711.
- Wilson, J. A. 1971. Early Tertiary vertebrate faunas, Vieja Group, trans-Pecos, Texas: Entelodontidae. *Pearce-Sellards Series* 17:1–17.
- Wilson, J. A. 1984. Vertebrate faunas 49 to 36 million years ago and additions to the species of *Leptereodon* (Mammalia: Artiodactyla) found in Texas. *Journal of Vertebrate Paleontology* 4: 199–207.
- Wilson, J. A. 1986. Stratigraphic occurrence and correlation of early Tertiary vertebrate faunas, trans-Pecos Texas: Agua Fria–Green Valley areas. *Journal of Vertebrate Paleontology* 6:350–373.
- Wilson, K. L. 1972. Eocene and related geology of a portion of the San Luis Rey and Encinitas quadrangles, San Diego County, California. M. S. Thesis, University of California, Riverside.
- Wortman, J. L. 1898. The extinct Camelidae of North America and some associated forms. *American Museum of Natural History Bulletin* 10:93–142.

