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SOUTHERN CALIFORNIA

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NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY

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GIANT ENTELODONT (MAMMALIA, ARTIODACTYLA) FROM THE EARLY MIOCENE OF SOUTHERN CALIFORNIA

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HUGH M. WAGNER³

ABSTRACT. We document upper cheek teeth of a giant entelodont, *Daeodon hollandi* (Peterson, 1905), from the Vaqueros Formation in the Santa Ana Mountains of southern California. The *Daeodon hollandi* specimen was associated with an assemblage of mollusks and marine and terrestrial vertebrates. The mollusks are characteristic of the west coast provincial "Vaqueros" molluscan stage, or early Miocene. The *Daeodon* and an associated small horse referred to *Parahippus paumiensis* Gidley, 1907, support an early Hemingfordian age. Another outcrop of the Vaqueros Formation within 10 km of Bolero Lookout has yielded a diverse fossil vertebrate assemblage that more clearly supports an early Hemingfordian age for the formation. Thus, the *Daeodon hollandi* from the Santa Ana Mountains represents one of the later occurrences of the species and extends its range into southern California.

INTRODUCTION

Entelodonts were a family of Eocene to Miocene large suiform artiodactyls, some with skulls nearly 1 meter long. They first appeared in North America during the late Eocene (Duchesnean) as immigrants from Asia (Brunet, 1979; Lucas, 1992). Entelodonts subsequently became relatively conspicuous members of latest Eocene–early Oligocene (Chadronian–Orellan) mammalian fossil assemblages in the western United States. They persisted through the late Oligocene into the early Miocene (Whitneyan–Hemingfordian), in part because a giant genus, usually called *Dinohyus* Peterson, 1905, represents a late lineage of Asian entelodonts that immigrated into North America near the end of the Oligocene (Brunet, 1979; Emry et al., 1995; Lucas and Emry, 1996; Lucas et al., 1996).

These last and largest North American entelodonts (Mammalia: Artiodactyla) are found in strata of late Oligocene (early Arikarean) to early Miocene (early Hemingfordian) age in Oregon, Wyoming, South Dakota, Nebraska, Texas, Alabama, Florida, South Carolina, and New Jersey (Sinclair, 1905; Peterson, 1909; Troxell, 1920; Allen, 1926; Frick, 1931; Simpson, 1930; Wilson, 1956, 1957; Parris and Green, 1969; Tedford et al., 1987; Westgate, 1992) (Fig. 1). Yet, despite their broad geo-

graphic and temporal (about 11 m.y.) ranges, these giant entelodonts are relatively rare as fossils. Complete skeletal material is known only from the lower part of the Harrison Formation at the Agate Spring fossil quarry, Sioux County, Nebraska (Peterson, 1909). The other records are confined to isolated teeth, skulls, jaws, or postcrania; at no locality are the giant entelodonts common as fossils. Here, we add to their record the upper cheek teeth of a giant entelodont from southern California (Fig. 2).

MATERIALS AND METHODS

One of the authors (HMW) collected LACM 140397, the upper cheek teeth of an entelodont described here and associated vertebrate fossils in May 1983. The entelodont specimen was measured with needle-point dial calipers and compared to other known upper cheek teeth of entelodonts described by Peterson (1909), Wilson (1957), Parris and Green (1969), and Westgate (1992).

In this article, the following institutional abbreviations are used: CM—Carnegie Museum of Natural History, Pittsburgh; LACM—Natural History Museum of Los Angeles County; SDSM—South Dakota School of Mines, Rapid City; TMM—Texas Memorial Museum, Austin; and USNM—National Museum of Natural History, Smithsonian Institution, Washington, D.C.

GEOLOGIC SETTING

The fossil occurrence is in the foothills of the Santa Ana Mountains of southern California (Fig. 2). The Santa Ana Mountains are within the Peninsular Range physiographic province, which is part of an active plate tectonic margin displaying both subduction and transform movements. The Santa Ana Mountains are a northward-plunging anticline that

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Figure 1. Map of the United States showing distribution of fossils of *Daeodon*. Localities are: 1, Unnamed unit above Haystack Valley Member, John Day Formation, Oregon. 2, Bolero Lookout, Vaqueros Formation, Santa Ana Mountains, California. 3, Big Badlands, South Dakota. 4, Lusk-Hat Creek Breaks, Wyoming. 5, Pine Ridge escarpment, Nebraska. 6, Agate Springs quarry, Nebraska. 7, Washington County, Texas. 8, San Jacinto County, Texas. 9, Vicksburg Group, Conecuh River, Escambia County, Alabama. 10, Franklin Phosphate Pit, Florida. 11, Ashley River Phosphates, South Carolina. 12, Farmingdale, New Jersey.

exposes primarily marine sedimentary rocks ranging in age from Jurassic to Pleistocene (Schoellhammer et al., 1981). The mountain range is uplifted on the east along the Elsinore fault zone (Lamar and Rockwell, 1986). Jurassic subduction along the

plate boundary produced a core of granitoid plutonics (Todd, 1994) and extrusive volcanic rocks (Santiago Peak Volcanics) intruding and overlying a modestly metamorphosed sequence of marine fore-arc sediments (Bedford Canyon Formation)



Figure 2. Location of the LACM giant entelodont site in the Vaqueros Formation at Bolero Lookout.

(Schoellhammer et al., 1981). The Cretaceous through Pliocene is represented by a discontinuous succession of primarily nearshore marine sediments. Formational boundaries are often abrupt, and nondepositional hiatuses exist between formations due to marine transgression and regression events associated with continued tectonics along the active Farallon/North American plate boundary (Schoellhammer et al., 1981; Belyea, 1984).

The entelodont *Daedon* and associated fossils were recovered from a badlands area below Bolero Lookout that developed in interbedded, variegated red beds and greenish to white sandstones generally referred to as the undifferentiated Sespe/Vaqueros formation (Schoellhammer et al., 1981). Nearly all variegated red beds in the Santa Ana Mountains and the Transverse Ranges of southern California are so identified (Lander, 1994b; Howard, 1988). This is common practice, even though the Sespe Formation was defined by Watts (1897) from its type locality along Sespe Creek, 160 km northwest of the Santa Ana Mountains, and the Vaqueros Sandstone was defined by Hamlin (1904) from its type locality in the mid-Coast Ranges of central California, 420 km northwest of the Santa Ana Mountains. Undifferentiated Sespe/Vaqueros formation rocks are exposed over a larger part of the northern Santa Ana Mountains than any other Mesozoic or Cenozoic rock unit. The undifferentiated Sespe/Vaqueros formation conformably overlies the middle Eocene Santiago Formation (Schoellhammer et al., 1981). The undifferentiated Sespe/Vaqueros formation is unconformably overlain by yellow to white, well-cemented, coarse marine sandstones of the middle Miocene (Temblor molluscan stage = Barstovian land-mammal age) Topanga Formation (Schoellhammer et al., 1981).

Although greenish marine sandstones referred to as Vaqueros Formation generally overlie variegated red sandstone/mudstone sequences referred to as Sespe Formation, at some localities the two lithofacies interdigitate (Schoellhammer et al., 1981). Marine invertebrates characteristic of the early Miocene "Vaqueros" provincial molluscan stage (Addicott, 1977) are fairly common in the Vaqueros lithofacies within the Santa Ana Mountains (Schoellhammer et al., 1981). Terrestrial vertebrates ranging in age from late Eocene (Uintan) (unpublished data from Eastern Transportation Corridor, Orange County Transportation Corridor Authority) to late early Miocene (early Hemingfordian) (Schoellhammer et al., 1981; Lander, 1994a) have been recovered from several areas within the red-bed "Sespe" lithofacies in the Santa Ana Mountains. Marine vertebrates (sharks, rays, and fishes) have also been recovered from the red-bed "Sespe" facies (see below).

Although existing geologic maps (Rogers, 1965; Schoellhammer et al., 1981) make no distinction between the Sespe and Vaqueros formations, Belyea (1984) and Belyea and Minch (1989) applied an extensive lithofacies approach to unravel the rela-

tionships between the Sespe and Vaqueros formations of the northern Santa Ana Mountains. They interpret the Vaqueros Formation as "a transgressive sequence of clastic marine shoreline deposits . . . (that) characterize the final phases of deposition in the northern Peninsular Ranges" (Belyea and Minch, 1989:297). They place the Bolero Lookout fossil occurrence within the Vaqueros Formation.

The crushed palate and upper dentition of *Daedon* was recovered from locality LACM(CIT) 449 near the zone of interdigitation between the continental facies of the Sespe Formation and the marine facies of the Vaqueros Formation. The specimen was in a mottled, light gray and tan, coarse arkosic sandstone. The mottled appearance of the sandstone was produced by marine bioturbation. The gray-green to tan, primarily coarse marine sediments continue stratigraphically upsection for approximately 20 meters, where they are capped by a resistant, light tan oyster bed that represents the base of the Topanga Formation in this region of the Santa Ana Mountains.

The associated vertebrate assemblage recovered from the deposits of the Vaqueros Formation below Bolero Lookout was collected from the same, approximately 1.5-meter thick, bioturbated sandstone as the *Daedon* palate and within 400 meters laterally of the fossil. The presence of marine bioturbation and the absence of articulated or associated vertebrate specimens suggest that the specimens were transported to shallow depths offshore before being deposited.

SYSTEMATICS

Class Mammalia Linnaeus, 1758

Order Artiodactyla Owen, 1848

Family Entelodontidae Lydekker, 1883

Genus *Daedon* Cope, 1878

REVISED DIAGNOSIS. *Daedon* is the largest entelodont known ($LP_4 = 45\text{--}53$ mm), and it is also distinguished from other entelodonts by the following combination of autapomorphic features: I_1^1 very small or absent, I^3 much larger than I^2 , incisor-canine diastema very short or absent, diastemata between all premolars, the largest of which is between the P^1 and the P^2 , lower molars with trigonids and talonids of subequal heights and lacking paraconids, alveolar border of premaxillary very short, jugal flange small, infraorbital foramen above posterior portion of P^3 , symphyseal tubercle very small or absent and large posterior tubercle (under P_4/M_1) on lower jaw, mandibular angle slopes gently posteriorly, trapezium absent, unciform completely separated from magnum by semilunar, metatarsal V absent, and fibula and tibia co-ossified (see Lucas et al., 1997).

DISCUSSION. The holotype of *Daedon shoshonensis* Cope, 1878, is part of the symphyseal re-

gion of the lower jaw and preserves crown fragments, roots, and/or alveoli of the left and right I_{1-3} , C 's, and P_{1-2} . Peterson (1909, fig. 18) previously illustrated the specimen and correctly noted that the I_1 is very small, I_3 is much larger than I_1 and larger than I_2 . There is no I_3 - C diastema, but P_1 and P_2 are separated by a diastema. No tubercle is present on the chin.

All these characteristics diagnose one genus of giant North American entelodonts to which the name *Dinohyus* is usually applied (Lucas et al., 1996, 1997). The holotype of the type species of *Dinohyus*, *D. hollandi*, displays all the features of the holotype of *Daeodon shoshonensis*, except that it has a very small tubercle on the chin. Size of the chin tubercle ranges from very small to absent in specimens we assign to *Daeodon*, quite different from the large chin tubercle found in *Archaeotherium* and similar North American entelodonts (Lucas et al., 1997). Therefore, we conclude that *Dinohyus* is a junior synonym of *Daeodon* (Lucas et al., 1996, 1997).

The holotype P_4 of *Ammodon leidymanus* Marsh, 1893, is very similar to the P_4 of the holotype of *Dinohyus hollandi* (compare illustrations in Marsh, 1893, and Peterson, 1909). The teeth only differ in the slightly larger size (about 15%), longer talonid (due to the larger posterior cingulid), and more prominent posterior ridges on the trigonid slope on the *A. leidymanus* holotype (also see Peterson, 1909: 68). The referred M_3 of *A. leidymanus* only differs from that tooth in the holotype of *D. hollandi* in being slightly longer (about 4%) and having a larger hypoconulid. We believe that these differences do not merit generic separation of the holotypes of *A. leidymanus* and *D. hollandi*, and they may not even merit separation at the species level. We thus consider *Dinohyus* and *Ammodon* to represent a single genus to which the senior synonym, *Daeodon*, should apply. We tentatively recognize *Daeodon leidymanus* and *Daeodon hollandi* as separate species pending greater knowledge of dental variability (especially of P_4). *Dinohyus* (?) *mento* Allen, 1926, here is assigned to *Daeodon* as *D. mento*.

Brunet (1979: 90) also recognized the close similarity of the type material of *Ammodon* and that of *Dinohyus* but chose to not synonymize the two genera because *Dinohyus* is based on more complete type material. We prefer to synonymize the two genera with the third, *Daeodon*.

There are four named species of *Daeodon*, the type species *D. shoshonensis* (Cope, 1878), *D. leidymanus* (Marsh, 1893), *D. hollandi* Peterson, 1909, and *D. mento* (Allen, 1926). Each species is based on one or a few specimens. Except for the holotype of *D. hollandi*, a complete skull and jaws, there is little morphological overlap of the holotypes of *Daeodon* species. Therefore, we find it difficult to evaluate the validity of these taxa and offer the following tentative, revised diagnoses:

1. *D. shoshonensis*—the smallest species of

Daeodon, possibly also distinguished by its lack of a chin tubercle.

2. *D. leidymanus*—a large species of *Daeodon* ($LP_4 = 52$ mm), also distinguished from *D. hollandi* by its larger, more cuspidate P_4 talonid and larger M_3 hypoconulid.

3. *D. hollandi*—a medium-sized species of *Daeodon* ($LP_4 = 45$ mm), also distinguished from *D. leidymanus* by its less cuspidate and smaller P_4 talonid and smaller M_3 hypoconulid and from *D. mento* by its nearly antero-posteriorly oriented P_1 .

4. *D. mento*—A large species of *Daeodon* distinguished from *D. hollandi* by its slightly larger size, one (not two) mental foramen, and the long axis of P_1 oriented at about 43° to the tooth row.

Daeodon hollandi is the most completely known and widely distributed species of *Daeodon*. Greater knowledge of dental variability in *Daeodon* probably will lead to synonymy of all four species under *D. shoshonensis* (Lucas et al., 1997).

Daeodon hollandi (Peterson, 1905) Figure 3A, B

REFERRED SPECIMEN. LACM 140397, nearly complete right P^3 - M^3 and less complete left P^3 - M^3 , originally found associated in a badly crushed palate and partial basicranium.

LOCALITY AND HORIZON. LACM(CIT) 449, Vaqueros Formation (see above).

DESCRIPTION. The P^3 is a two-rooted tooth. The roots are massive, arranged antero-posteriorly under the crown, and the posterior root is much broader and shows incipient division into two roots (medial and lateral). The crown is a single, thick, pyramidal cusp that is slightly curved lingually. The lingual surface has a basal cingulum and thick, low, longitudinal enamel ridges that run from the cingulum toward the cusp apex. The labial surface has an incipient basal cingulum but smooth enamel. The apex of the cusp is worn at the tip, exposing a small, circular area of dentine. The posterior crown base is broken and incomplete—evidently the posterior cingulum is missing. Measurements of the P^3 and other teeth are listed in Table 1.

The P^4 is a triangular tooth in occlusal view with three stout roots—two labially and a larger one lingually. The labial portion of the crown is dominated by a tall, blunt paracone with a worn tip exposing a circular area of dentine. Lingual to that cusp is a much lower protocone with a much larger dentine exposure because of wear. The wear surface on the paracone is inclined antero-lingually, whereas that on the protocone is inclined postero-lingually. The P^4 has a cingulum continuous around the crown except on most of the labial aspect. Blunt, thick ridges or beads of enamel rise from this cingulum toward the paracone and the protocone, especially on the posterior and the lingual edges of the crown. A narrow, shallow cleft separates the paracone and the protocone. The parastyle is very

Table 1. Measurements (in mm) of upper cheek teeth of selected specimens of *Daedon*.

	LACM	CM 1594	SDSM 675 ¹	TMM 40223-1 ²	USNM 25809 ³
P ³ L	43.9	43.5	48.0	—	—
P ³ W	32.8	33.2	27.0	—	—
P ⁴ L	39.6	37.2	34.0	41.0	38.2
P ⁴ W	44.6	38.6	37.0	45.5	39.9
M ¹ L	47.6	42.9	42.0	45.8	45.5
M ¹ W	49.7	44.8	45.0	50.0	46.1
M ² L	48.4	45.2	46.0	—	—
M ² W	56.4	47.3	49.0	—	—
M ³ L	45.5	42.7	—	—	—
M ³ W	51.2	46.5	—	—	—

¹From Parris and Green (1969); measurements only to the nearest millimeter.

²From Wilson (1957).

³From Westgate (1992).

small, and the metastyle is distinct and relatively large.

The M¹ is the most worn tooth, with extensive dentine exposure on the crown. The tooth is four-rooted, with nearly equal-sized roots under each corner of the crown, which has a trapezoidal occlusal outline. The tooth is bilophed, with two parallel lophs running labio-lingually—an anterior loph that connects the paracone and the protocone and a posterior loph connecting the metacone and the hypocone. There is a complete cingulum anteriorly, labially, and posteriorly. A slight ectoflexus is just anterior to the metacone. Of the four principal cusps, the protocone appears to have been the largest, but it is totally obliterated by wear. The paracone is slightly larger than the metacone. A shallow trigon basin lies between and lingual to the paracone and the metacone.

The M² is similar to the M¹ but larger and with: (1) a more prominent parastyle; (2) a lingual cingulum extending anteriorly from the hypocone; (3) a very prominent antero-lingual cingulum; (4) a less worn crown; and (5) a more shallow ectoflexus located more anteriorly, so it is just posterior to the paracone.

The anterior half of the M³ closely resembles the M². However, the tooth has a much smaller and more lingually placed metacone than does the M¹ or the M². The hypocone is also smaller and more labially positioned than the M¹ or the M² hypocone. Wear on the hypocone has exposed a small, circular area of dentine on the cusp apex. A small, circular dentine exposure antero-labial to the hypocone is the metaconule. The M³ is four rooted and has an incomplete lingual cingulum. It is slightly smaller than the M² but slightly larger than the M¹.

DISCUSSION. Lucas et al. (1996, 1997) revised the generic level taxonomy of the North American giant entelodonts and assigned them to *Daedon*

Cope 1878 (= *Ammodon* Marsh, 1893; = *Dinohyus* Peterson, 1905). Large size and crown morphology preclude assigning the LACM specimen to any entelodont genus other than *Daedon*. In size and morphology, the specimen is closest to *D. hollandi* (Fig. 3; also see Peterson, 1909, pls. 55, 57, 58). However, several differences are apparent: (1) the LACM specimen has a P³ with a more posteriorly deflected principal cusp, ribbed enamel and a (possibly) smaller talonid heel; (2) the P⁴ of the LACM specimen has broader anterior and posterior slopes and a more prominent metastyle; (3) the M¹ of the LACM specimen has a more prominent ectoflexus and wider posterior and labial cingula; (4) the M² of the LACM specimen has a more prominent labial cingulum; (5) the M¹⁻³ of the LACM specimen are more transverse teeth (relatively wider and shorter; Table 1); and (6) the LACM M³ has a more prominent labial cingulum.

It could be argued that these differences warrant species-level separation of the LACM specimen from *D. hollandi*. However, only a limited basis exists for assessing dental variability in *Daedon*. The only population sample—from the Agate Springs fossil quarry—preserves only one upper dentition (Peterson, 1909). Other known upper cheek teeth of *Daedon*—from Texas (Wilson, 1957), South Dakota (Parris and Green, 1969), and Alabama (Westgate, 1992)—represent a range of metric (Table 1) and meristic variation that encompasses the holotype of *D. hollandi* and the LACM specimen. Indeed, the LACM specimen most closely resembles the upper cheek teeth of *Daedon* from Texas (Wilson, 1957, fig. 1), especially in the triangular occlusal outline of the P⁴, the position and depth of the M¹ ectoflexus, and the relatively transverse proportions. Therefore, we act conservatively and assign the LACM specimen to *Daedon hollandi*.

ASSOCIATED FAUNA

As reported in Schoellhammer et al. (1981) and Belyea and Minch (1989), the Bolero Lookout locality LACM(CIT) 449 has yielded a sparse assemblage of both marine and terrestrial vertebrates. The only terrestrial vertebrates reported in the Schoellhammer et al. study were camel tooth fragments and an incomplete first phalanx that G. Edward Lewis compared to *Paratylopus primaevus* (Schoellhammer et al., 1981: D36). This material has not been relocated or reexamined for this study. One of us (HMW) collected the site again in May 1983 and recovered a more diverse assemblage than was reported in Belyea (1984) and Belyea and Minch (1989). With assistance from others, the assemblage has been reexamined by one of us (DPW) and found to be more diverse than previously reported (Table 2).

Elasmobranch chondrichthyans are represented by a single tooth each of *Heterodontus* sp. (LACM 140704), *Carcharinus* sp. (LACM 140705), *Galocercus* sp. (LACM 140706), *Isurus* sp. (LACM

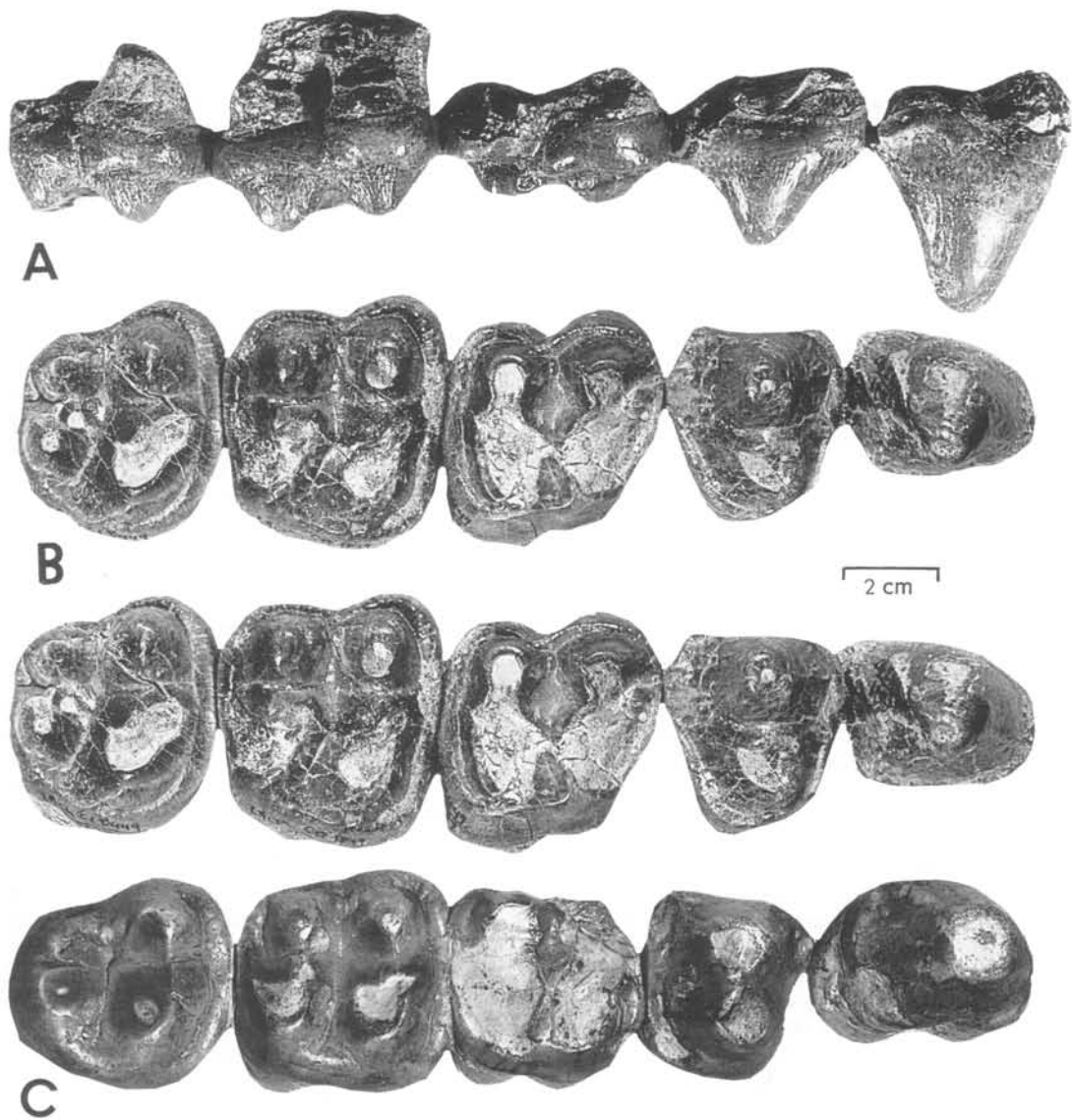


Figure 3. *Daeodon hollandi* upper cheek teeth. A, B, LACM CIT(449)/140397, labial (A) and stereo occlusal (B) views of right P³-M³. C, CM 1594, holotype of *D. hollandi*, occlusal view of right P⁴-M³.

29681), and an undetermined genus and species of megachasmid (LACM 140707). The ray *Myliobatis* sp. is represented by three partial teeth (LACM 140708-104710) and nine partial caudal spines (LACM 140711-140718). Identifications of elasmobranchs were provided by J.D. Stewart.

A cheloniid sea turtle is represented by three associated and one isolated carapace fragments (LACM 29699, LACM 29700) and one first costal plate (LACM 29701). Identifications of chelonians were provided by S.A. McLeod.

An undetermined genus and species of mysticete whale is represented by a fragment of lumbar vertebra (LACM 29696). An odontocete whale is rep-

resented by an involucrum of a left tympanic bulla (LACM 140719). Identifications of cetaceans were provided by L.G. Barnes.

With the exception of the *Daeodon*, the most diagnostic mammalian specimen from the assemblage is an unworn right upper third molar of a small brachyodont horse (LACM 140724) that closely resembles *Parahippus pawniensis* Gidley, 1907. The specimen is subquadrate in occlusal outline, with the posterior cingulum narrower than the proto-loph, a configuration characteristic of the third molar. The proto-loph and metaloph are connected to the ectoloph. The ectoloph bears a distinct mesostyle and a smaller metastyle. There are weak ribs

Table 2. Composite faunal list of locality LACM(CIT) 449.

Class Chondrichthyes
Order Galeomorpha
Family Heterodontidae
<i>Heterodontus</i> sp.
Family Carcharhinidae
<i>Carcharhinus</i> sp.
<i>Galeocerdo</i> sp.
Family Lamnidae
<i>Isurus</i> sp.
Family Megachasmidae
genus and species not determined
Order Batoidea
Family Myliobatidae
<i>Myliobatis</i> sp.
Class Reptilia
Order Chelonia
Family Cheloniidae
genus and species not determined
Class Mammalia
Order Perissodactyla
Family Equidae
<i>Parahippus pawniensis</i> Gidley, 1907
Order Artiodactyla
Family Entelodontidae
<i>Daedon hollandi</i> (Peterson, 1905)
Family Camelidae
cf. <i>Michenia</i> sp.
Order Cetacea
Family Mysticetidae
genus and species indeterminate
Family Odontoceti
genus and species indeterminate

on both the paraconule and metaconule. The protoleph bears a distinct protoconule. A well-developed crochet projects anteriorly from the middle of the metaloph to the base of the protoconule. The well-developed crochet distinguishes the specimen from species of *Mesohippus* Marsh, 1875, and *Miohippus* Marsh, 1874. There is also a right lower equid canine (LACM 140725) and right equid astragalus (LACM 29676) in the assemblage that are here referred to *Parahippus* Leidy, 1858.

Although previously reported in Belyea and Minch (1989), no material clearly referable to a rhinoceros is present in the assemblage. The camel material examined by Lewis in 1955 (Schoellhammer et al., 1981) has not been reexamined. Additional material herein referred to *Michenia* sp. includes a right cuboid (LACM 140720), proximal phalanx (LACM 140721), partial calcaneus (LACM 29678), and two partial upper molars (LACM 140722, LACM 140723). This material is not definitive, but it is most consistent with small, brachyodont camels like *Michenia* Frick and Tay-

lor, 1971. Well-preserved material of the same size and general configuration recovered from the undifferentiated Sespe/Vaqueros formation approximately 10 km away is clearly referable to *Michenia* (Lander, 1994a).

AGE AND CORRELATION

As reported in Schoellhammer et al. (1981), the invertebrate fossils recovered from the upper part of the undifferentiated Sespe/Vaqueros formation (Vaqueros Formation of Belyea and Minch, 1989) in the vicinity of Bolero Lookout include the gastropods *Rapana* sp. cf. *R. vaquerosensis* and *Turritella inezana santana* and the pelecypods *Anadara* sp. cf. *A. santana* and *Here excavata*. Within the well-characterized West Coast provincial molluscan stages, *Rapana vaquerosensis* and *Turritella inezana* are guide fossils of the early Miocene "Vaqueros" provincial molluscan stage (Addicott, 1977).

The occurrence of a rare terrestrial fossil mammal taxon in a marine sedimentary unit is valuable with regard to cross-correlation of marine and non-marine biochronology. At the Bolero Lookout locality LACM(CIT) 449, the *Daedon hollandi* fossil was recovered from the marine Vaqueros Formation and associated with the small equid *Parahippus pawniensis*. The joint occurrence of these two species of fossil mammals suggests a correlation with the early portion of the Hemingfordian land-mammal age (compare Tedford et al., 1987).

The fossil mammalian taxa represented in the Bolero Lookout assemblage closely resemble those observed in the collections of the University of California, Berkeley, Museum of Paleontology (UCMP) in the Flint Hill local fauna from the Batesland Formation of South Dakota. Therefore, the Bolero Lookout and Flint Hill local faunas are here considered to be essentially temporal equivalents.

During development of the North American land-mammal "ages" by the Wood Committee (Wood et al., 1941), the Sespe/Vaqueros fossil vertebrate localities of the Santa Ana Mountains in the California Institute of Technology (now housed at LACM) were utilized by Chester Stock to correlate between the Miocene Pacific marine megainvertebrate biostratigraphy and the terrestrial fossil mammal assemblages of the John Day Formation in Oregon and those of the central plains of the United States. The occurrence of temporally restricted taxa, such as *Daedon* and *Parahippus*, enables a significant refinement of the age determinations for the deposits from which they were recovered. As indicated by Minch and Belyea (1989), the occurrence of *Daedon* at the Bolero Lookout locality in the Santa Ana Mountains allows a more specific age determination for the contact between the Sespe Formation and the Vaqueros Formation in southern California.

Deposits of the upper undifferentiated Sespe/Vaqueros formation at the Santiago Canyon Landfill, 10 km northwest of Bolero Lookout, have yielded

a diverse assemblage of both larger fossil vertebrates (turtles, canids, felids, artiodactyls, and perissodactyls) and smaller fossil vertebrates (sharks, fish, lizards, snakes, insectivores, lagomorphs, and rodents) (Lander, 1994a). Based on faunal comparisons, Lander (1994a) concluded that the fossil assemblage from the Santiago Canyon Landfill is earliest Hemingfordian in age. The only taxa in common between the Santiago Canyon Landfill and Bolero Lookout localities are the small shark, *Carcharhinus*, and possibly the small camel, *Michenia*. Additional material collected from the undifferentiated Sespe/Vaqueros formation at the Santiago Canyon Landfill and additional materials collected from other landfills and highway construction projects that are currently unavailable for study may contain additional taxa in common with the Bolero Lookout locality. All available evidence supports an early Hemingfordian age for the mammal fossils from the Vaqueros Formation at Bolero Lookout.

In the United States, *Daedodon* has its first occurrence during the early Arikareean (late Oligocene) and last occurrence during the early Hemingfordian (early Miocene) (Tedford et al., 1987). This gives the genus a chronologic range of about 11 million years, from 18 to 29 Ma. The oldest records of *Daedodon* are in the early Arikareean of Wyoming-Nebraska, though its occurrence in Alabama may be equally old (Westgate, 1992). The youngest records are in the Hemingfordian of Oregon, California, and Texas. The precise ages of *Daedodon* occurrences in South Carolina and Florida are poorly constrained. *Daedodon* clearly had a broad distribution across the United States by the late Arikareean. This distribution is consistent with immigration of the genus from Asia via Beringia during the early Arikareean.

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LITERATURE CITED

Addicott, W.O. 1977. Neogene chronostratigraphy of nearshore marine basins of the eastern North Pacific. In *Proceedings, First International Congress on Pacific Neogene Stratigraphy*, 151-175. Tokyo: Kaiyo Shuppan Co., Ltd.

Allen, G.M. 1926. Fossil mammals from South Carolina. *Bulletin of the Museum of Comparative Zoology* 67: 447-467.

Belyea, R.R. 1984. *Stratigraphy and depositional environments of the Sespe Formation, northern Peninsular*

Ranges, California. Masters thesis, Department of Geology, San Diego State University, 206 pp.

Belyea, R.R., and J.A. Minch. 1989. Stratigraphy and depositional environments of the Sespe Formation, northern Santa Mountains, California. In *Conglomerates in basin analysis: A symposium dedicated to A.O. Woodford*, ed. I.P. Colburn, P.L. Abbott, and J.A. Minch. Pacific Section, Society of Economic Paleontologists and Mineralogists, vol. 62, 281-300.

Brunet, M. 1979. Les grand mammifères chefs de file de l'immigration Oligocène et le problème de la limite Éocène-Oligocène en Europe. Paris: Éditions de la Fondation Singer-Polignac, 281 pp.

Cope, E.D. 1878. On some of the characters of the Miocene fauna of Oregon. *Proceedings of the American Philosophical Society* 18:63-78.

Emry, R.J., S.G. Lucas, and B.U. Bayshashov. 1995. Early Oligocene entelodont from the Zaysan basin, eastern Kazakhstan. *Selevinia* 3:3-6.

Frick, C. 1931. Childs Frick's explorations for 1931. *Natural History* 31:668-669.

Gidley, J.W. 1907. Revision of the Miocene and Pliocene Equidae of North America. *Bulletin of the American Museum of Natural History* 23:865-934.

Hamlin, H. 1904. Water resources of the Salinas Valley, California. *U.S. Geological Survey Water-Supply Paper* 89:1-91.

Howard, J.L. 1988. Sedimentation of the Sespe Formation in southern California. In *Santa Barbara and Ventura Basins: Tectonics, structure, sedimentation, oil-fields along an east-west transect*, ed. A.G. Sylvester and G.C. Brown. South Coast Geological Society Field Guide, vol. 64, 53-69.

Lamar, D.L., and T.K. Rockwell. 1986. An overview of the tectonics of the Elsinore fault zone. In *Neotectonics and faulting in Southern California*, ed. P.L. Ehlig. Cordilleran Section, Geological Society of America, Guidebook and Volume, field trip numbers 10, 12, 18, 149-158.

Lander, E.B. 1994a. Paleontologic resource impact mitigation program final report; Santiago Canyon Landfill, southeast and southwest borrows, Orange County, California. Prepared for County of Orange Integrated Waste Management Department, 55 pp.

Lander, E.B. 1994b. Recalibration and causes of marine regressive-transgressive cycle recorded by middle Eocene to lower Miocene nonmarine Sespe Formation, southern California continental plate margin. In *Sedimentology and paleontology of Eocene rocks in the Sespe Creek area, Ventura County, California*, ed. A.E. Fricke. Pacific Section, Society for Sedimentary Geology, vol. 74, 79-88.

Linnaeus, C. 1758. *Systema naturae per regna tria natural, secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis, locis*. Editio decima, reformata, vol. 1. Stockholm: Laurentii Salvii, 824 pp.

Lucas, S.G. 1992. Redefinition of the Duchesnean land mammal "age," late Eocene of western North America. In *Eocene-Oligocene climatic and biotic evolution*, ed. D.R. Prothero and W.A. Berggren, 88-105. Princeton: Princeton University Press.

Lucas, S.G., and R.J. Emry. 1996. Late Eocene entelodonts (Mammalia: Artiodactyla) from Inner Mongolia, China. *Proceedings of the Biological Society of Washington* 109:397-405.

Lucas, S.G., S. Foss, and R.J. Emry. 1996. Giant Oligo-Miocene entelodonts from the United States. *Geo-*

- . 1997. Taxonomy and distribution of *Daeodon*, a giant Oligocene-Miocene entelodont (Mammalia, Artiodactyla) from the United States. *Proceedings of the Biological Society of Washington*, in review.
- Lydekker, R. 1883. Siwalik selenodont Suinae. *Palaeontologica Indica* 10(2):146.
- Marsh, O.C. 1893. Description of Miocene Mammalia. *American Journal of Science* 146:407–412.
- Owen, R. 1848. Description of the teeth and portions of jaws of two extinct anthracotheroid quadrupeds (*Hyopotamus vectianus* and *Hyop. bovinus*) discovered by the Marchioness of Hastings in the Eocene deposits of the N. W. coast of the Isle of Wight: With an attempt to develop Cuvier's idea of the classification of the pachyderms by the number of their toes. *Quarterly Journal of the Geological Society of London* 4:103–141.
- Parris, D.C., and M. Green. 1969. *Dinohyus* (Mammalia: Entelodontidae) in the Sharps Formation, South Dakota. *Journal of Paleontology* 43:1277–1279.
- Peterson, O.A. 1905. A correction of the generic name (*Dinochoerus*) given to certain fossil remains from the Loup Fork Miocene of Nebraska. *Science* 22: 719.
- . 1909. A revision of the Entelodontidae. *Memoirs of the Carnegie Museum* 4:41–158.
- Rogers, T.H. 1965. *Geologic map of California, Santa Ana sheet*. California Division of Mines and Geology.
- Schoellhammer, J.E., J.G. Vedder, R.F. Yerkes, and D.M. Kinney. 1981. Geology of the northern Santa Ana Mountains, California. *U.S. Geological Survey Professional Paper* 420-D:D1–D109.
- Simpson, G.G. 1930. Tertiary land mammals of Florida. *Bulletin of the American Museum of Natural History* 59:149–211.
- Sinclair, W.J. 1905. New or imperfectly known rodents and ungulates from the John Day Series. *Bulletin, Department of Geology, University of California* 4: 125–143.
- Tedford, R.H., M.F. Skinner, R.W. Fields, J.M. Rensberger, D.P. Whistler, T.E. Galusha, B.E. Taylor, J.R. MacDonald, and S.D. Webb. 1987. Faunal succession and biochronology of the Arikareean through Hemphillian interval (late Oligocene through earliest Pliocene deposits) in North America. In *Cenozoic mammals of North America: geochronology and biostratigraphy*, ed. M.O. Woodburne, 153–210. Berkeley: University of California Press.
- Todd, V.R. 1994. The peninsular ranges batholith from western volcanic arc to eastern mid-crustal intrusive and metamorphic rocks, San Diego County, California. In *Geological investigations of an active margin*, ed. S.F. McGill and T.M. Ross. Geological Society of America, Cordilleran Section Guidebook, 27th Annual Meeting, 227–235.
- Troxell, E.L. 1920. Entelodonts in the Marsh collection. *American Journal of Science* 50(4):243–255, 361–386, 431–445.
- Watts, W.L. 1897. Oil and gas yielding formations of Los Angeles, Ventura and Santa Barbara Counties. *California State Mining Bureau Bulletin* 11:1–94.
- Westgate, J.W. 1992. *Dinohyus* aff. *D. hollandi* (Mammalia, Entelodontidae) in Alabama. *Journal of Paleontology* 66:685–687.
- Wilson, J.A. 1956. Miocene formations and vertebrate biostratigraphic units, Texas Coastal Plain. *American Association of Petroleum Geologists Bulletin* 40: 2233–2246.
- Wilson, J.A. 1957. Early Miocene entelodonts, Texas coastal plain. *American Journal of Science* 255:641–649.
- Wood, H.E., 2nd, R.W. Chaney, J. Clark, E.D. Colbert, G.L. Jepsen, J.B. Reeside, and C. Stock. 1941. Nomenclature and correlation of the North American continental Tertiary. *Bulletin of the Geological Society of America* 52:1–48.

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