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TAXONOMIC REVISION OF THE MIDDLE EOCENE (UINTAN-DUCHESNEAN) PROTOCERATID *LEPTOREODON* (MAMMALIA: ARTIODACTYLA)

JOSHUA A. LUDTKE AND DONALD R. PROTHERO

Department of Geology, Occidental College, Los Angeles, California 90041

Abstract—The primitive hornless protoceratid *Leptoreodon* occurs abundantly in the Uintan (Utah, southern California, Saskatchewan, Trans-Pecos Texas, Wyoming, and Montana) and rarely in the Duchesnean (southern California, Texas, Saskatchewan). Large new collections of *Leptoreodon* from the middle Eocene rocks of San Diego County, California, prompted a re-examination of the systematics of the genus. Early Uintan localities yield the large type species, *L. marshi*, the diminutive *L. pusillus*, and the largest species, *L. major*. All of these species are still valid, distinguishable by size and by the presence of anterior and posterior cingulids on the lower molars of *L. major*. Late Uintan localities produce all seven known species: the rare *L. edwardsi*, the large *L. stocki*, the sharp-crested *L. leptolophus*, plus *L. major, L. marshi, L. pusillus*, and a new species, *L. golzi*, morphologically similar to *L. leptolophus* but distinctly smaller in size. Early Duchesnean localities yield the common species *L. leptolophus* and a few *L. stocki* and *L. pusillus*. Large new samples of *L. leptolophus* show that it can be consistently distinguished from *L. edwardsi* based on the gently curved anterior crest on p4; the crest in *L. edwardsi* is sharply inflected lingually. More subtle characters differentiate *L. stocki* from *L. leptolophus*, but the two remain statistically distinguishable. There is slight sexual dimorphism in the upper canines, although the sample size of good skulls is still small. This is consistent with the pattern in many other hornless artiodactyls, such as tragulids and moschids.

Key words: *Leptoreodon*, Eocene, Uintan, Duchesnean, Artiodactyla, Protoceratidae, California

INTRODUCTION

Leptoreodon was a primitive middle Eocene member of the family Protoceratidae, a group of tylopod artiodactyls that sported a variety of peculiar cranial appendages in the more derived Oligocene and Miocene forms (Prothero, 1998). These appendages included forked horns on the nasals or over the occiput, short paired knobs over the nasals and frontals, and long curved horns over the orbits. However, all the early members of this family were hornless. *Leptoreodon* was one of the most common artiodactyls in the middle Eocene. It first appeared during the early Uintan North American land-mammal "age" (NALMA) and last appeared in early Duchesnean. [Note: in the pre-1990s literature, the Uintan was considered late Eocene, and the Duchesnean was thought to be latest Eocene or earliest Oligocene. However, recent argon/argon dating and magnetic stratigraphy, summarized by Prothero and Emry, 1996, have shown that both land mammal "ages" are late middle Eocene in age.] During the early Uintan, *Leptoreodon* ranged widely from southern California, to Utah, Saskatchewan, Texas, and Montana. Some of the species persisted into the early Duchesnean, after which the genus became extinct.

In the more than hundred years since its initial discovery and description, the genus has been augmented with five additional species, all of which were originally based on specimens from southern California. The current research was triggered by the addition of hundreds of new specimens (including skulls and jaws) from the recent excavations in San Diego County (now stored in the San Diego Natural History Museum). This new material more than tripled the total sample size, and so necessitated a re-examination of all the named species to see if they are still valid in light of the new collections. Unfortunately, the postcranial skeleton of *Leptoreodon* is still known only from a few fragments, so this study will necessarily concentrate on cranial and dental material.

MATERIALS AND METHODS

We examined hundreds of specimens in several museums (AMNH, LACM, SDNHM, UCMP, UCR), using dial calipers to measure the available tooth and skull dimensions. Data were statistically analyzed and plotted on Excel spreadsheets. Specimens were photographed with a Nikon 5700 digital camera.

Institutional abbreviations: AMNH = American Museum of Natural History, New York; LACM = Natural History Museum of Los Angeles County, Los Angeles; LACM(CIT) = California Institute of Technology collection (now curated at the LACM); NMC = National Museum of Canada, Ottawa; NMNH = National Museum of Natural History, Smithsonian Institution, Washington, D.C.: ROM = Royal Ontario Museum, Toronto; SDNHM, San Diego Natural History Museum, San Diego; SMNH, Saskatchewan Museum of Natural History, Regina; UCMP = Museum of Paleontology, University of California, Berkeley; UCR = University of California, Riverside, vertebrate collection (now curated at the UCMP); YPM-PU, Princeton University collections (now curated at the Peabody Museum of Natural History, Yale University, New Haven, Connecticut).

SYSTEMATIC PALEONTOLOGY

Order Artiodactyla Owen, 1848

Suborder Tylopoda Illiger, 1811

Family Protocratidae Marsh, 1891

Leptoreodon Wortman, 1898

Camelomeryx Scott, 1898
Merycodesmus Scott, 1898
Hesperomeryx Stock, 1936

Type species—*L. marshi* Wortman, 1898

Included species—*L. edwardsi* Stock, 1936; *L. major* Golz, 1976; *L. pusillus* Golz, 1976; *L. leptolophus* Golz, 1976; *L. stocki* Kelly, 1990; *L. golzi* new species.

Distribution—Early Uintan to Duchesnean, California, Texas, Utah, Saskatchewan, Wyoming, and Montana.

Diagnosis—Primitive hornless protoceratid distinguished from the more primitive *Leptotragulus* by the large bulbous metaconid and the broadly flexed anterior crest on p4. The talonid basin on p4 is closed posteriorly. Distinguished from more advanced protoceratids in lacking an anteriorly projecting p4 metaconid.

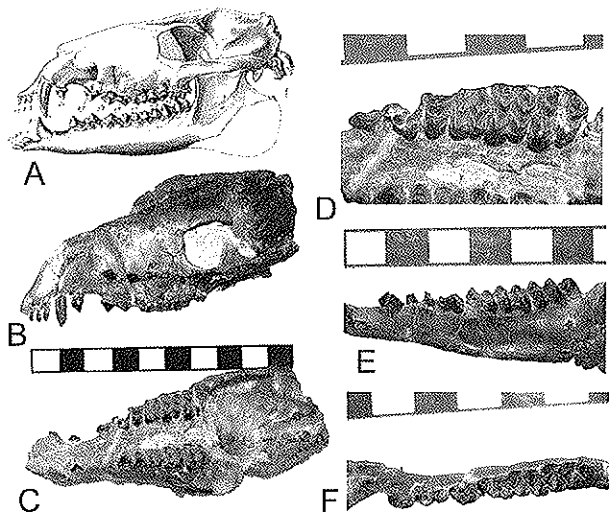

FIGURE 1. *Leptoreodon marshi*, type specimen (AMNH 2064). **(A)** Wortman's (1898) original illustration. **B-F.** Current views of the specimen in (B) lateral view of skull; **(C)** palatal view of the skull; **(D)** crown view of upper teeth; **(E)** lateral view of lower jaw; **(F)** crown view of lower teeth. Scale bar in cm.

Discussion—*Leptoreodon marshi* was described by Wortman (1898) based on a partial skull, rami, and fragments of the skeleton (AMNH 2064) from White River Pocket, in Uinta Formation member B, Uinta County, Utah (Fig. 1). Noting the D-shaped cross-section of the upper canines and the caniniform p1, Wortman thought it resembled an oreodont, hence the name *Leptoreodon*. However, he also noted that it has diastemata around the P1 and p1, more slender limbs, and a more slender skull than any known oreodont, and so placed the taxon in the Camelidae. Just six days after Wortman's paper appeared, Scott (1898) published on specimens in the Princeton collection from the Uinta Basin. He named an almost complete skull (YPM-PU 11225) *Merycodesmus gracilis*, and a partial cranium (YPM-PU 11226) *Camelomeryx longiceps*. Apparently, Scott was unaware of Wortman's simultaneous work, and so could not realize that they were looking at the same taxon. However, he did correctly suggest that his specimens might be related to *Protoceras* and not to oreodonts.

Stock (1936) described a large new collection of teeth, jaws, and fragmentary postcranials from the Tapo Ranch l.f. in the Sespe Formation as *Leptoreodon* (*Hesperomeryx*) *edwardsi*. He based the new subgenus on subtle differences in the teeth that Golz (1976) did not think worthy of subgeneric status. In his discussion of this material, Stock correctly realized that *Leptoreodon* was not an oreodont, but thought that it was a leptomerycid ruminant instead.

Gazin (1955) reviewed of all the known later Eocene artiodactyls of North America, and formally synonymized Scott's (1898) *Merycodesmus gracilis* and *Camelomeryx longiceps* with *Leptoreodon marshi*. He also clarified the distinctions between *Leptoreodon* and the more primitive *Leptotragulus*, but thought that both were primitive leptomerycid ruminants (he also regarded the protoceratids *Poabromylus* and *Heteromeryx* as leptomerycids). However, he still regarded these forms as ancestral to the protoceratids, because at that time the protoceratids were thought to be related to ruminants, not camelids.

Wilson (1974) described several specimens from the Uintan of Trans-Pecos Texas as *Leptoreodon marshi* based on their prominent p4 metaconids. Wilson (1974) agreed with Scott (1898) that *Leptoreodon* was a protoceratid, not an oreodont or leptomerycid. Patton and Taylor (1973) confirmed that *Leptoreodon* and *Leptotragulus* were protoceratids.

Golz (1976) comprehensively reviewed the Eocene artiodactyls of southern California, and sank Stock's (1936) *Hesperomeryx*. He named a number of new species (*L. major, L. pusillus, L. leptolophus*) from the middle Eocene of southern California; these species will be discussed in greater detail below. After Golz's (1976) paper, some of his species were recognized outside of California. Wilson (1984) listed *L. major, L. pusillus, L. leptolophus* and *L. edwardsi* from the Uintan and Duchesnean of Trans-Pecos Texas. Wilson (1984) and Westgate (1990) referred specimens from the late Uintan Laredo Formation of the Texas Gulf Coastal Plain to *L. pusillus* and *L. leptolophus*. Black (1978) reported *Leptoreodon* sp. from the Uintan of the Badwater area in Wyoming, although he was not convinced that *Leptoreodon* was distinct from *Leptotragulus*. Storer (1984) reported on teeth of *L. marshi* from the Uintan Swift Current Creek local fauna of Saskatchewan, and in 1993 Storer reported *Leptoreodon* sp. from the Duchesnean Lac Pelletier local fauna of Saskatchewan. Tabrum et al. (1996) also reported *L. marshi* from the Uintan of Montana.

Finally, Kelly (1990) studied large new collections from the Sespe Formation in Ventura County, California, and named a new species, *L. stocki*, based on specimens that Golz (1976) had referred to *L.* aff. *L. leptolophus*.

Leptoreodon marshi Wortman, 1898

Figures 1-2

Holotype—AMNH 2064, a skull, rami, vertebrae, and limb fragments, from the early Uintan White River Pocket, Uinta "B" member, Uinta Basin, Utah (Fig. 1).

Hypodigm—from the Uinta Formation, member B: YPM-PU 11225 (type of *Merycodesmus gracilis*); YPM-PU 11226 (type of *Camelomeryx longiceps*); AMNH 2064, 1807, 1816, 1985; USNM 20397, left ramus with p4-m3, right ramus with p4; from LACM(CIT) loc. 249, Friars Formation, San Diego County, California: LACM 26331, p4; LACM 26334, p4-m3; LACM 26335, p4-m3; LACM 26336, p4; LACM 26339, m2; from miscellaneous UCMP and UCR Friars localities: UCMP 95793, m1-m3; UCMP 95794, m1-m2; UCMP 113258, p4-m3; from the early Uintan Whistler's Squat l.f., Trans-Pecos Texas: TMM 41372-44, p4-m3; TMM 41372-391, p4; TMM 41372-395, m2-m3; TMM 41372-412, p4-m3; TMM 41372-417, p4-m3; TMM 41372-419, p4-m1; TMM 41372-178, lower jaw with p2-m3; TMM 41372-177, skull fragment with dP2-4M1; TMM 41372-176, lower jaw with dp1-4m1=2; TMM 41372-175, skull fragment with C-P3, M1-3; from the early Uintan Swift Current Creek l.f., Saskatchewan: dozens of specimens in the ROM, NMC, and SMNH collections listed by Storer (1984, p. 87); uncatalogued specimens from the late Uintan Douglass Draw l.f. of Montana (Tabrum et al., 1996); from the early Duchesnean Candelaria l.f., Trans-Pecos, Texas: TMM 40689, P3-M3, p2-3;

Distribution—Early Uintan, Uinta Formation member B, Utah; Friars Formation, San Diego County, California; Whistler's Squat l.f., Texas; Swift Current Creek l.f., Saskatchewan; late Uintan, Douglass Draw l.f., Montana; early Duchesnean, Candelaria l.f., Texas.

Diagnosis—Large (Fig. 2) *Leptoreodon* (slightly smaller than *L. major*, but larger than the remaining species) with an abruptly inturned anterior extremity of the anterior crest of p4, a raised crescent near the entoconid position in p4, and weak or absent cingulids on the lower molars (in contrast to the distinct cingulids on the lower molars of *L. major*).

Discussion—The type species of the genus is still easily distinguished by its relatively large size (Fig. 2) in comparison to every other species except *L. major*, and by the weak or absent cingulids on the lower molars (which distinguish it from *L. major*). The lower p4 is also distinctive, with a crescentic crest in the entoconid position and an abruptly inturned anterior extremity of the anterior crest (Fig. 3). The type specimen, although not as well preserved as Wortman's (1898) original illustration suggests (Fig. 1), still clearly shows a relatively large upper canine, so it probably represents a male individual.

L. marshi, although not as abundant in the early Uintan as *L. major*, is nevertheless common in the Friars Formation of San Diego

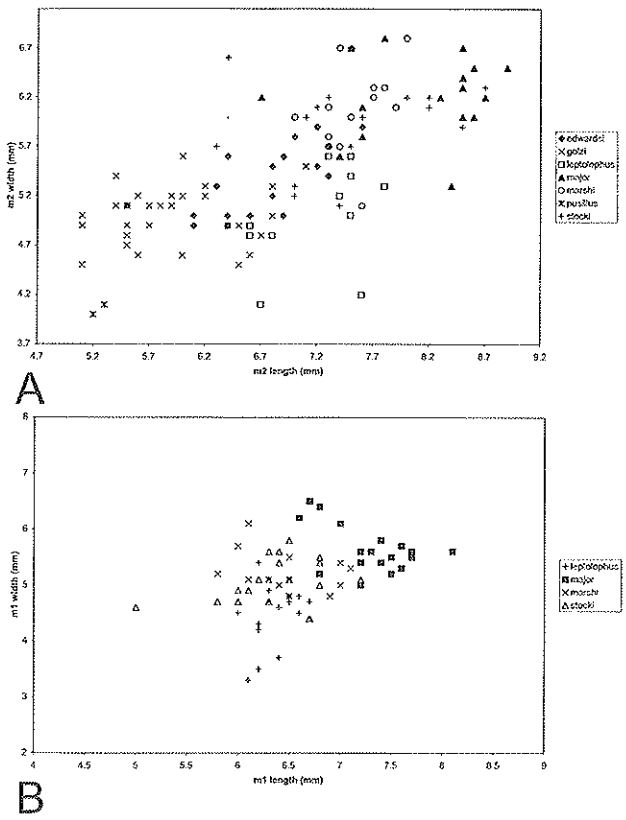

FIGURE 2. (A) Bivariate plot of m2 dimensions of all species of *Leptoreodon* discussed in this study. The largest species (*L. major*) plots at the large end of this distribution, followed by the slightly smaller *L. stocki* and *L. marshi*. *L. leptolophus* and *L. edwardsi* plot in the middle of the distribution, with *L. golzi* at the small size range. *L. pusillus* is disjunctly smaller. (B) Bivariate plot of m1 dimensions of the larger species of *Leptoreodon*. *L. major* again plots at the large end of the cluster, with *L. stocki*, *L. marshi*, and *L. leptolophus* overlapping in size just below *L. major*.

County, the lower Uinta Formation of Utah, the early Uintan of Texas, and the Swift Current Creek l.f. of Saskatchewan. It also occurs in the late Uintan of Montana, and the Duchesnean of west Texas.

Leptoreodon major Golz, 1976

Figures 2, 4

Holotype—LACM 27400, a right dentary with damaged root of p1, damaged and unerupted p2, and dp3-m3, from LACM(CIT) loc. 249-P, early Uintan, Friars Formation, San Diego County, California (Fig. 4).

Hypodigm—From the Friars Formation, San Diego County, California: LACM 26326, m2-m3; LACM 26327, p4-m3; LACM 26328, p4-m2; LACM 26329, p4-m3; LACM 26330, p4; LACM 27401, m1-m3; SDNHM 47857, p4-m3; SDNHM 47878, cranium with left C-M3, right C; SDNHM 54856, p4-m3; SDNHM 55906, m1-m3; SDNHM 55911, p4-m2; SDNHM 55924, p4-m3; SDNHM 55925, m1-m3; SDNHM 55926, m1-m3; SDNHM 55927, m1-m3; SDNHM 55929, p4-m1; SDNHM 55930, p4-m1; SDNHM 78821, m1-m2; TMM 41672-179, m2; UCMP 113266, m1-m2; UCMP 113277, m1-m3. From the early Uintan Whistler Squat l.f., Trans-Pecos Texas: TMM41466-2, right maxilla with M1-3; TMM 41466-13, left ramus with m1-2; From the late Uintan Serendipity l.f., Trans-Pecos Texas: TMM41672-83, right M1 or M2; TMM 41672-179, ramus with m2.

Distribution—From the early Uintan of San Diego County and Trans-Pecos Texas, and the late Uintan of Trans-Pecos Texas.

Diagnosis—Differs from all other species of *Leptoreodon* in its large size, stronger cingula and styles on the upper molars, and well-developed anterior and posterior cingulids on the lower molars.

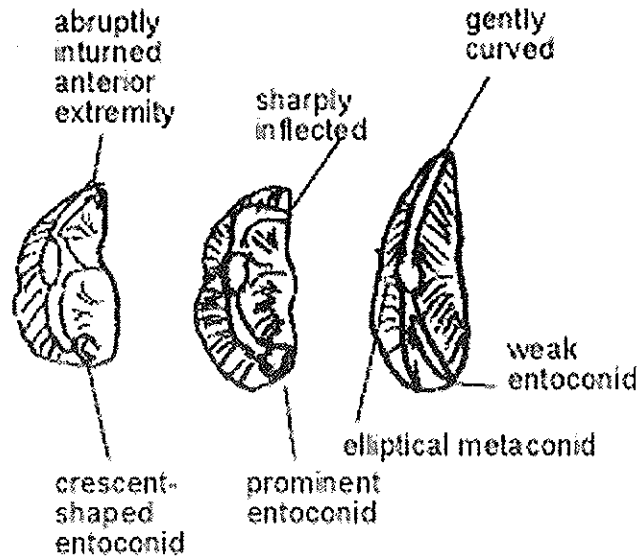

FIGURE 3. Sketches (from tracings of photographs) of crown views of the p4 in selected species, showing distinctive characters mentioned in text. Anterior is to the top, and lingual is to the right. (left) *L. marshi*. (center) *L. edwardsi*. (right) *L. leptolophus*.

Description—Most of the new materials from the SDNHM collections add only slightly to the descriptions by Golz (1976), except for one specimen. SDNHM 47878 includes a skull, mandible, and partial skeleton that appear referable to *L. major*. Although badly crushed, SDNHM 47878 (Fig. 4B-D) is a complete skull that displays not only the first view of the cranium of the species, but also a more complete upper tooth row. The large size of the canines suggests that it is from a male individual. The skull is badly crushed dorsoventrally, so most of the surface is covered with tiny fractures, and sutures are difficult to determine. However, the general features of the skull can be determined where they are not crushed or broken.

Compared to the type skull of *L. marshi* (AMNH 2074—Fig. 1) and the skull of *Leptotragulus* (MCZ 5304—Norris, 2000, fig. 2) in dorsal view (Fig. 4B), *L. major* has a longer, narrower rostrum, and a posterodorsally extended occipital region. The sagittal crest is much stronger than in *L. marshi*, but about the same state as in *Leptotragulus*, and the lambdoid crest is prominent and flares posterodorsally. The sagittal crest splits anteriorly into prominent supraorbital crests above the braincase, which are not so prominent in *L. marshi* or in *Leptotragulus*. These crests also flare broadly over the orbit, with a small dorsal postorbital process that is unconnected with the zygoma, so there is no postorbital bar.

The frontal area is broad and diamond shaped, with a slight depression or concavity in front of the orbits. There are small elongate pits along the posterior end of the nasal-maxillary suture, presumably for some kind of facial nerve opening. The long rostrum also flares laterally at its anterior end, with broad flanges on the anterior end of the maxilla for the large canines. The premaxillae are damaged, but the I1-3 are visible on the left side. They are tiny, spatulate teeth that are strongly procumbent.

In lateral view (Fig. 4C), the high sagittal crest can be clearly seen, as well as the posterior overhang of the lambdoid crest. The orbit is slightly dorsoventrally crushed, but otherwise is very similar to the condition in *L. marshi* and *Leptotragulus*. The facial region of the maxilla is too badly crushed to determine if there was a preorbital fossa, as in *Leptotragulus*. The canines are much larger proportionally than they

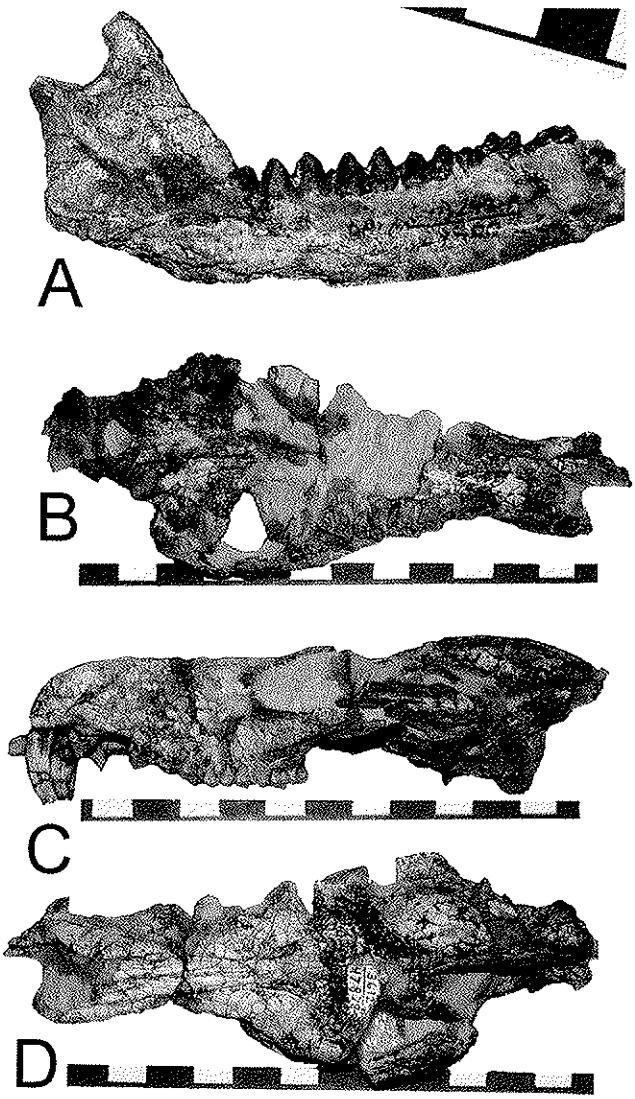

FIGURE 4. *Leptoreodon major*. (**A**) Type specimen (LACM 27400). (**B-D**) Referred skull (SDNHM 47878) in (B) palatal; (C) lateral; and (D) dorsal views. Scale bar in cm.

are in the presumed male specimen of *L. marshi*, or the presumed male specimen of *Leptotragulus*, so this canine enlargement is more than just sexual dimorphism.

The basicranial region (Fig. 4D) is too badly damaged to identify many features, although the occipital condyles are thin and narrow, and the post-tympanic process and postglenoid process can be recognized from their broken basal regions. The glenoid fossa is relatively shallow, but laterally broad on the base of the zygoma. Most of the palatine region is too badly damaged to discuss, but there do not appear to be any foramina in the palate posterior to the canines.

In addition to the anterior dentition, SDNHM 47878 has a large, bladelike p1, with a short diastema between it and the canine, and a long diastema between p1 and p2. The p2 is also bladelike, but with a slightly triangular crown view due to the enlarged metaconid. The remaining premolars and molars on this specimen are too worn to say much about their condition, but as far as they are preserved, they are indistinguishable from the type of *L. major*. In many features of the p4, *L. major* is one of the most primitive (although the largest) species of *Leptoreodon*, as previously stated by Golz (1976, p. 2) and Wilson (1984, p. 203).

The large upper canines in SDNHM 47878 appear to reflect a common trend in the Protoceratidae. Scott (1898), in his initial description of *Merycodesmus gracilis*, remarked on the seemingly vestigial nature of upper canines in females of *Protoceras*, while the males exhibited both large canines and horns. *Leptoreodon* does not have horns, but the known male skulls do seem to show large canines, often two to three times the size of the upper first premolar. The trend towards large canines is paralleled by the development of large caniniform lower first premolars. Unfortunately, SDNHM 47878 lacks a lower jaw to comment on this trend in *L. major*.

Discussion—*Leptoreodon major* is easily distinguished from all other species of *Leptoreodon* by its disjunctly larger size (Fig. 2), although small individuals are close to *L. marshi* in size. *L. major* is also recognized by the distinct cingulids on the lower molars, a feature not seen in *L. marshi*.

Most of the specimens of *Leptoreodon major* were recovered from the early Uintan Friars Formation of San Diego County, California (Walsh, 1996; Walsh et al., 1996). However, several specimens described by Wilson (1984) came from the early Uintan Whistler's Squat l.f. and from the late Uintan Serendipity l. f. of Trans-Pecos Texas. *L. major* is not as widespread in the early Uintan as *L. marshi*, since it has not been reported from the Uinta Basin or from Saskatchewan yet.

Leptoreodon edwardsi (Stock, 1936)

Figures 5-6

Leptoreodon (Hesperomeryx) edwardsi Stock, 1936
Leptoreodon edwardsi: Golz, 1976

Holotype—LACM(CIT) 1839, right P2-M3, from the late Uintan LACM(CIT) loc. 180, Tapo Canyon l.f., Sespe Formation, Simi Valley, California (Fig. 5).

Paratype—LACM(CIT) 1840, incomplete left ramus with p2-m3 (Fig. 4).

Hypodigm—From the type locality: LACM 1946, p4; LACM 27371, p4-m3; LACM 27372, p4-m3; LACM 27373, p4-m3; LACM 27374, p4-m3; LACM 27375, p4-m3; LACM 27377, m1; LACM 27571, paired p4-m3; LACM 45696, p4-m2; LACM 45697, p4-m2; LACM 45698, p4-m2; LACM 45712, p4-m2; LACM 45714, p4-m2; LACM 45715, p4-m2; LACM 45716, p4-m2; LACM 45717, p4-m2; LACM 45719, p4-m2; LACM 45721, p4-m3; LACM 45748, m1-m3; LACM 45749, m1-m3; LACM 45750, m1-m3; UCMP 72155, 72156, 72157. From the late Uintan Serendipity l.f., Trans-Pecos Texas: numerous specimens listed by Wilson (1984, p. 204).

Distribution—From the late Uintan of southern California and Trans-Pecos Texas.

Diagnosis—*Leptoreodon edwardsi* is a medium-sized species of *Leptoreodon* (Fig. 6) distinguished from similar-sized *L. leptolophus* in having a sharp lingual inflection (Fig. 3) of the anterior crest of the p4 (a derived character). *L. leptolophus* and most other species of *Leptoreodon* have a gently curved lingual inflection of the anterior crest of p4. For this reason, the p4 in *L. edwardsi* appears slightly shorter and wider in proportions (Fig. 3). Compared to *L. leptolophus, L. edwardsi* also has slightly broader upper and lower teeth with stronger cingula and cingulids and weaker crests; a more sharply recurved metastyle on M3; a more bulbous paraconid and metaconid on p4; and a stubbier posterior lobe on m3, which is rarely completely closed. *L. edwardsi* is easily distinguished by size from the larger species *L. major* and *L. marshi*, and from the smaller species *L. pusillus*.

Description—In California, *L. edwardsi* is still known only from the type locality, Tapo Canyon, in the Sespe Formation, and little new material has been reported since the detailed descriptions by Golz (1976), so no further description is warranted here.

Discussion—Although we were initially reluctant to separate such similar-sized contemporaneous species, close examination of the collections confirms that the medium-sized late Uintan (Tapo Canyon) Sespe *Leptoreodon* (*L. edwardsi*) are easily distinguished from their

FIGURE 5. *Leptoreodon edwardsi*. Paratype specimen (LACM(CIT) 1840). Scale bar in cm.

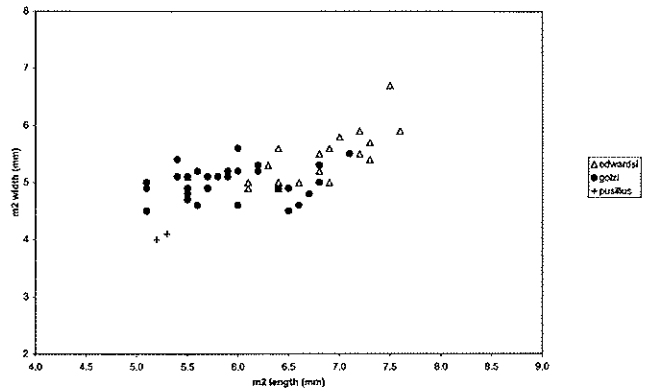

FIGURE 6. Bivariate plot of m2 dimensions of smaller species of *Leptoreodon*. *L. edwardsi* is at the larger end (overlapping with the larger species), followed by the smaller *L. golzi*, and the disjunctly smaller *L. pusillus*.

contemporaries in San Diego County (*L. leptolophus*). So far as we can tell, in California the specimens with the sharply inflected anterior p4 crest (*L. edwardsi*) are restricted to Tapo Canyon, while *L. leptolophus* is known primarily from San Diego County in the late Uintan. Thus, we are confident that the species are distinct, and worth retaining. In Texas, *L. edwardsi* is also reported from the late Uintan Serendipity l.f. (Wilson, 1984).

Leptoreodon leptololphus Golz, 1976

Figures 6-7

Holotype—UCR 13499, which includes left C-M3, right P1-M3, left p2-m3, right p1-m3, and fragments of the skull. From the late Uintan or early Duchesnean Laguna Riviera Quarry (UCR locality RV-6830), Santiago Formation, San Diego County, California (Fig. 7).

Hypodigm—From the late Uintan or early Duchesnean, San Diego County, California: LACM 24505, m1; LACM 24506, p4-m1; LACM 26344, p4-m3; UCMP 82554, m1; UCMP 83152, p4-m3; UCMP 83155, m1; UCMP 83156, m1-m2; UCR 12839, m1; UCR 13447, m1-m2; UCR 13993, m1-m3; UCR 13997, m1; UCR 14000, m1-m2; UCR 14001, m1-m3; UCR 14013, m1; UCR 14021, m2; UCR 14501, m2. Many additional specimens are listed by Golz (1976), as well as dozens of new specimens from member C of the Santiago Formation localities in the UCMP and SDNHM collections. From the late Uintan Laredo Formation, Webb County, Texas: TMM 41871-1, ramus with p4-m3; 42486-571, maxilla with P4-M3; 42486-321, maxilla with M2-3; 42486-347, maxilla with M1-2; 42486-309, M1; plus numerous additional isolated teeth (Westgate, 1990, p. 464). From the early Duchesnean Candelaria l.f., Trans-Pecos Texas: TMM40276-17, ramus with p1-m3; TMM 40689-1, fragmentary P3-M3, lower c, p2-3.

Distribution—From the late Uintan and/or early Duchesnean, San Diego County, California, and Webb County, Texas, and the early Duchesnean, Trans-Pecos Texas.

Diagnosis—Medium-sized *Leptoreodon* with a gently curved anterior crest (Fig. 3) on the p4 (compared to the sharply lingually inflected crest on *L. edwardsi*). Differs from all other species of *Leptoreodon* in having weaker cingula and cingulids, and stronger, more slender crests on the teeth, more sharply compressed styles on the molars, less bulbous paraconid and metaconid on p4 (which appear as bulges on the anterior and posterolingual crests instead), and a more slender and elongate posterior lobe on m3. The upper molars tend to be transversely compressed. Differs from *L. marshi* and *L. major* in its smaller size, and from *L. pusillus* by its larger size.

Description—Although abundant new material is now available in the SDNHM collections, it duplicates the material already described by Golz (1976), so we found no new features that were worthy of description.

Discussion—*L. leptolophus* is primitive with respect to the condition of the anterior p4 crest (compared to similar-sized *L. edwardsi*), but it is highly derived in having much more elongate and slender and sharper crests on the teeth, which easily distinguish it from most other species, as Golz (1976) noted. The large new samples from the SDNHM collections in the Santiago Formation of San Diego County further confirm this distinction. Wilson (1984) and Westgate (1990) were able to confirm the distinctiveness of this species when new specimens were found in two different regions of Texas.

Although *L. leptolophus* is similar in size to *L. edwardsi*, they apparently did not overlap in geographic range. During the late Uintan, *L. edwardsi* was found mainly in the Sespe Formation of California, and in the Serendipity l.f. of Trans-Pecos Texas, while *L. leptolophus* was restricted to San Diego County, and the Texas Gulf Coastal Plain. In the Duchesnean, *L. leptolophus* appears in Trans-Pecos Texas, but is extinct elsewhere (as is *L. edwardsi*).

Leptoreodon pusillus Golz, 1976

Figures 6, 8

Holotype—UCR 14005, a left ramus with p2-m3; from the late Uintan or early Duchesnean (Walsh et al., 1996; Prothero, 2001) Laguna Riviera Quarry (UCR loc. RV-6830), Santiago Formation (member C), San Diego County, California (Fig. 8).

Hypodigm—From the type locality: LACM 42401, p4-m1; LACM 128904, m2-m3. From the late Uintan Laredo Formation, Webb County, Texas: TMM 42486-224, M1; 42486-352, upper molar fragment; 42486-216, lower molar fragment (Westgate, 1990). From the early Uintan Whistler Squat l.f., Trans-Pecos Texas: TMM 41444-1, p3; 41443-304, 41443-268, lower molar fragments; 41443-10, astragalus. From the late Uintan Serendipity l.f., TMM 41549-6, lower molar fragments.

Distribution—From the early Uintan, Trans-Pecos Texas, and the Texas Gulf Coastal Plain; from the late Uintan-early Duchesnean, San Diego County, California, and Trans-Pecos Texas.

Diagnosis—*L. pusillus* is distinguished from all other species of *Leptoreodon* by its small size (Fig. 6). It is even smaller than the smallest species of *Leptotragulus, L. clarki*. In addition to size, it differs from the larger *L. edwardsi* and *L. leptolophus* in lacking a lingual root on P2, more broadly based styles on the upper molars, a weaker hypoconid on p4, and more conical lingual cuspids on the lower molars. A number of other features were cited by Golz (1976, p. 62), al-

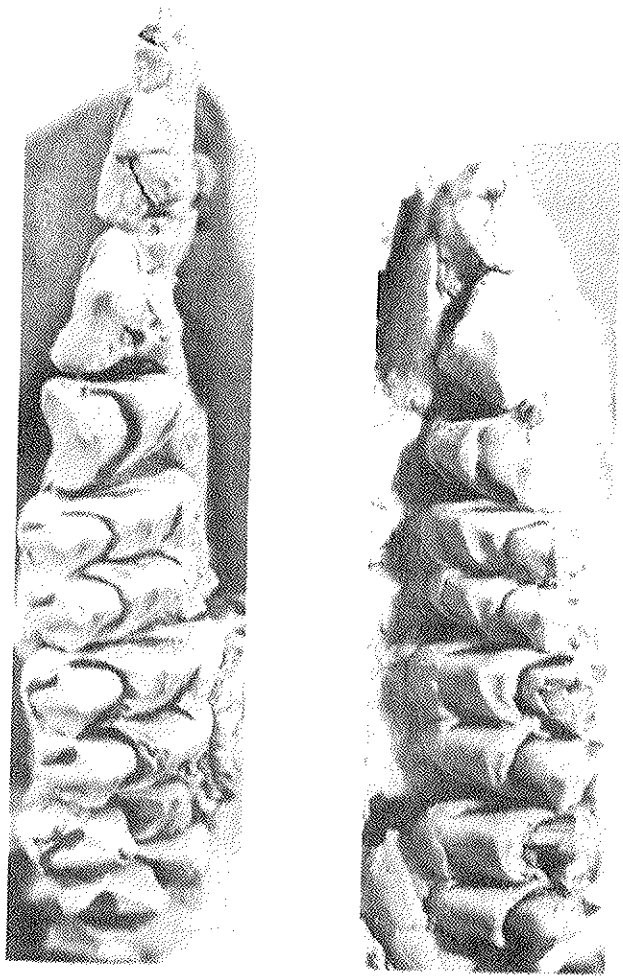

FIGURE 7. *Leptoreodon leptolophus* (left) Type specimen (UCR 13499) and (right) referred maxilla (LACM 26344) (after Golz, 1976).

though many of these proved to be more variable and difficult to ascertain.

Description—Relatively little new material of *L. pusillus* has turned up, despite the larger collections. None were present in the new samples in the SDNHM collections, and the new specimens from Texas (Wilson, 1984; Westgate, 1990) add nothing to the descriptions of Golz (1976), so no new descriptions are required here.

Discussion—*L. pusillus* easily stands out from the other species of *Leptoreodon* by its small size (Figs. 2, 6). Surprisingly, even though it is distinct and easy to recognize, no new specimens have turned up in the large collections recently recovered in San Diego County. The only new material reported since Golz (1976) occurred in the Uintan and Duchesnean of Texas (Wilson, 1984; Westgate, 1990).

Leptoreodon stocki Kelly, 1990

Figures 2, 9

Leptoreodon sp., aff. *L. leptolophus* Golz, 1976

Holotype—LACM 26368, partial left dentary with p4-m3, from the late Uintan Brea Canyon l.f., Sespe Formation, Simi Valley, California (Fig. 9).

Hypodigm—LACM (CIT) 477, m1-m3; LACM (CIT) 1948, p4-m2; LACM 27389, p4-m2; LACM 27390, p4; LACM 27391, m3; LACM 27392, p4-m3; LACM 27393, m2-m3; LACM 27394, p4-m3; LACM 27395, p4, m2; LACM 27396, m3; LACM 52207, m1; LACM 52208, m2-m3; LACM 55191, m1-m2; LACM 55192, m1-m2; LACM 55194, m1-m2; LACM 55195, p4-m1; LACM 128891, m1; LACM 128896, m1-m2; LACM 128905, p4-m2; LACM 128907, paired p4-m3; LACM 128912, p4; LACM 128913, m1-m3; TMM 40276-17, p4-m3; TMM 41871-1, p4-m3.

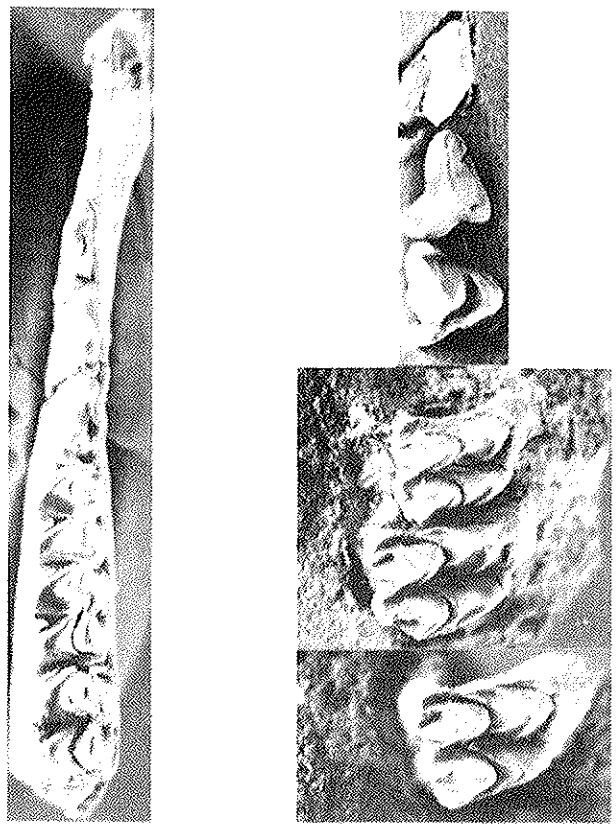

FIGURE 8. *Leptoreodon pusillus* (left) Type specimen (UCR 14005) and (right) referred upper teeth (UCR 80839) (after Golz, 1976).

Distribution—From numerous late Uintan and early Duchesnean localities, Sespe Formation, Simi Valley, California (see Kelly, 1990, p. 16, for details).

Diagnosis—*Leptoreodon stocki* is about equal in size to *L. marshi*, but smaller than *L. major*. Compared to most other species of *Leptoreodon*, the teeth have stronger and more slender crests, and the molar mesostyles and metastyles are more sharply flexed. The p4 paraconid and metaconid are less bulbous, and the p4 is wider and less reduced relative to m1. The m3 hypoconulid is more slender and anteroposteriorly elongated, with an accessory cuspulid that is posterolingually directed and crescent-shaped. A number of other characters were cited by Kelly (1990, p. 16), but these are the most consistently diagnostic features in our opinion.

Description—No new material has been reported since Kelly (1990), so no further descriptions are needed here.

Discussion—*L. stocki* is difficult to separate from *L. leptolophus*, since both have stronger and more slender crests compared to other species of *Leptoreodon*. The biggest difference is the slightly larger size of *L. stocki* (5-19% larger, according to Kelly, 1990), and the configuration of the m3 hypoconulid. *L. stocki* is also restricted to the Sespe Formation, while *L. leptolophus* occurs in San Diego County and in Texas.

Leptoreodon golzi n. sp.

Figures 6, 10

Holotype—SDNHM 47921, crushed skull with canines through

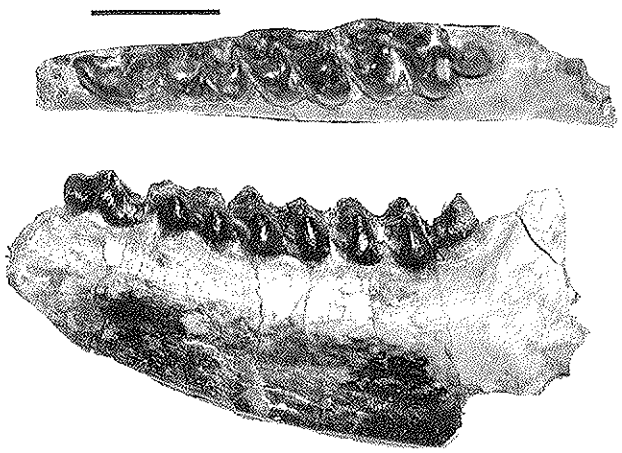

FIGURE 9. *Leptoreodon stocki*. Type specimen (LACM 26368).

M3 on both sides (Fig. 9), from Jeff's Discovery (SDNHM loc. 3276), late Uintan, Santiago Formation (member C), northern San Diego County, California (Walsh, 1996) (Fig. 10A-B).

Paratype—SDNHM 47704, pair of rami with p1-m3 on the right ramus, c-m3 on the left ramus (Fig. 10C).

Hypodigm—SDNHM 32164, p4-m3; SDNHM 40842, paired p4-m3; SDNHM 40855, p4-m3; SDNHM 40863, p4-m2; SDNHM 40865, p4-m3; SDNHM 40872, p4-m3; SDNHM 40873, p4, m2-m3; SDNHM 40874, p4-m1; SDNHM 40893, p4-m3; SDNHM 40894, p4-m2; SDNHM 42622, p4-m2; SDNHM 43764, p4-m2; SDNHM 43768, p4-m3; SDNHM 47419, p4-m3; SDNHM 47968, p4-m3; SDNHM 48130, p4-m2; SDNHM 48176, p4-m3; SDNHM 48214, p4-m2; SDNHM 48265, p4-m3; SDNHM 48318, p4-m1; SDNHM 48451, p4-m3; SDNHM 48518, p4; SDNHM 48597, p4-m3; SDNHM 48932, p4-m1; SDNHM 48949, p4; SDNHM 60966, p4-m3; SDNHM 60968, p4-m3; SDNHM 60973, p4-m3; SDNHM 60979, p4-m2; SDNHM 85111, p4-m3; SDNHM 85112, p4-m2.

Etymology—In honor of David Jon Golz. In his relatively brief period in the field of vertebrate paleontology, he revolutionized our understanding of the fauna of the Eocene in southern California.

Distribution—From the late Uintan (Santiago Formation, member C, and Mission Valley Formation), San Diego County, California.

Diagnosis—Small-sized (Fig. 6) species of *Leptoreodon*, smaller than *L. major, L.marshi, L. stocki, L. leptolophus, L.edwardsi,* but larger than *L. pusillus*. Crests of the upper and lower teeth are sharp, and the teeth relatively narrow, as in *L. leptolophus*, but disjunctly smaller in size. The p4 has a gently curved anterior crest, although it is more lingually inflected than the crest in *L. leptolophus*, but not as sharply bent as in *L. edwardsi*.

Description—The type specimen (Fig. 10A-B) of *L. golzi* (SDNHM 47921) is a badly crushed skull of a male individual, judging from the large canines. The right maxilla has been sheared so that it lies in the plane of the left maxilla, and most of the rest of the skull is too badly damaged to interpret.

There are no incisors preserved, but the canines are large and laterally compressed, with a strong posterior curvature. There is a short diastema between the canine and P1. P1 is a stubby, triangular, blade-like tooth, with a sharp anterior edge and a blunt posterior edge. A long diastema separates P1 from P2. The P2 is also a triangular blade, with a small low cingulum on the anterior basal portion, and a slightly basined posterior ridge. P3 is strongly triangular in crown view, but the crown of the tooth is so worn that only faint traces remain of the anterior and posterior ridges. There is a small posterointernal cingulum on the protocone, but otherwise the tooth is featureless. P4 is more quadrangular in crown view, with a strong, worn selene connecting the paracone and metacone, and a weak selene in the protocone position. It bears weak anterior and posterior lingual cingula, but no labial cingula.

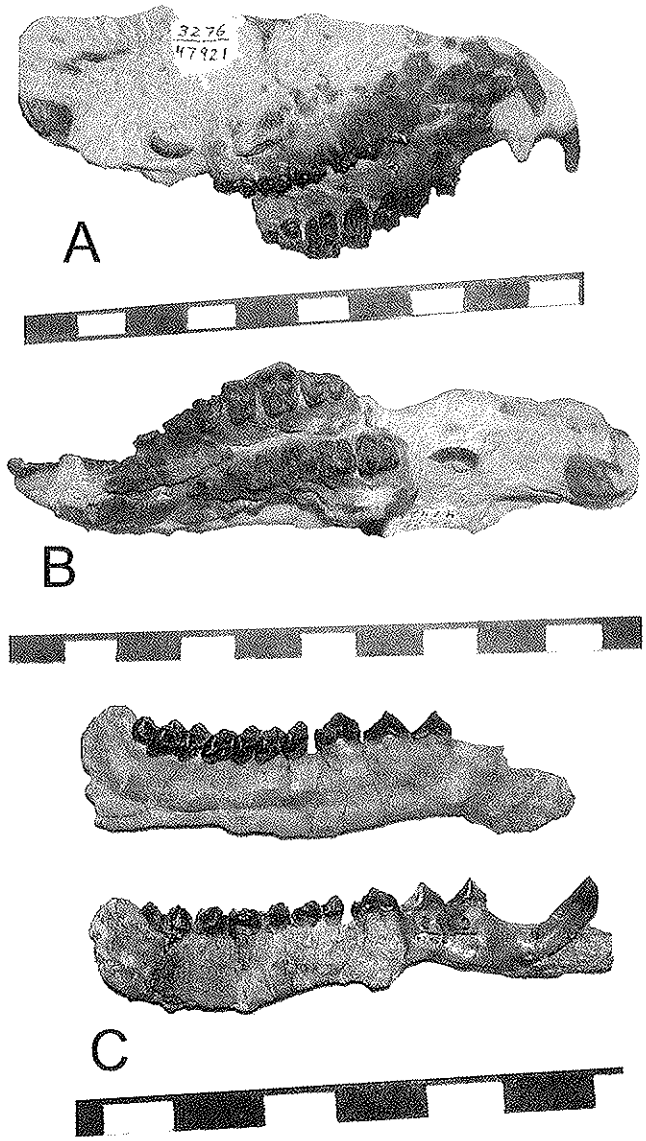

FIGURE 10. *Leptoreodon golzi* n. sp. (A-B) Type specimen (SDNHM 47921) in (**A**) lateral and (**B**) palatal views. (**C**) Paratype rami (SDNHM 47704). Scale bar in cm.

M1 is very worn, but traces of the selenes on the protocone, metacone, paracone, and metaconule are still visible. There is a weak cingulum in the valley between the protocone and metaconule, and a faint labial cingulum. M2 is slightly less worn than M1. It bears strong selenes on the paracone, metacone, protocone, and metaconule, well-developed anterior and posterior cingula, and separate lingual cingula on the protocone and metaconule. There is a strong style on the labial face of the protocone, and weaker style on the metacone. M3 is the least worn tooth, and shows four well-developed selenes on the paracone, metacone, protocone, and metaconule. The metaconule selene is much smaller than that of the protocone, making the tooth more like a quadrilateral than a rectangle. There is a strong lingual cingulum wrapped all the way around the protocone, and a smaller weaker lingual cingulum around the metaconule. Labial cingula are prominent on the paracone and metacone, as are well-marked styles on the labial

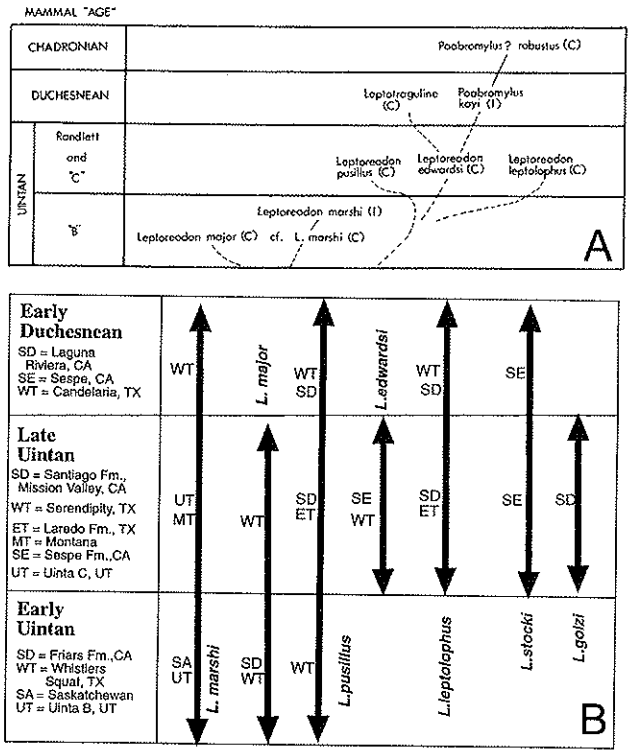

FIGURE 11. (**A**) Golz's (1976, fig. 33) portrayal of protoceratid phylogeny, based on materials known at the time. (**B**) Present distribution of the species of *Leptoreodon*, based on recent discoveries.

surfaces. Most of the rest of the skull is too badly damaged to interpret, but there is a deep anterior-facing preorbital fossa just above the P2 on both sides of the specimen.

The lower teeth are best represented by another specimen, SDNHM 47704 (Fig. 10C). The incisors and canines are not preserved, but the caniniform p1 is large and laterally compressed, and slightly procumbent. Judging from its relative size, it probably came from a male individual as well. There is a long diastema between the p1 and p2. The p2 is a large triangular blade, with sharp anterior and posterior ridges. The p3 is also long and bladelike, but there is a small trigonid basin developed on the posterior ridge. The p4 is somewhat less bladelike than p1 or p2, but it still has a strongly developed anterior ridge, which is only slightly curved in the lingual direction (more than in most specimens of *L. leptolophus,* but not curved as sharply as the anterior ridge in *L. edwardsi*). The p4 has a well developed lingual and labial ridges on the posterior edge that enclose a small talonid basin. There is a faint crescent-shaped metaconid on the p4, but it is not as strong as in *L. leptolophus*. The m1 is very worn, but the selenes on the trigonid and talonid are still visible despite the wear. It has no lingual cingula, but a small labial cingulum between the trigonid and talonid. The m2 has well developed selenes on the trigonid and talonid, and a strong labial cingulum between them. The m3 bears two well-developed selenes, with a strong labial cingulum between the trigonid and talonid. The hypoconulid is deeply basined, closed on all sides (unlike the hypoconulid in some other species of *Leptoreodon*).

Discussion—Large samples of late Uintan *Leptoreodon* from the Santiago Formation of northern San Diego County were originally labeled "*L.* cf. *edwardsi*" or "*L.* sp." because their teeth were not as slender and bladelike as typical *L. leptolophus* from the latest Uintan/Duchesnean of San Diego County. In examining these specimens more closely, we found that they are also smaller than any other species of *Leptoreodon* except *L. pusillus*. If these specimens are lumped in with the Duchesnean sample of *L. leptolophus* from the Santiago Formation, the sample size has an unacceptably large coefficient of variation (>10) in most variables, suggesting that possibly two species are present.

The anterior crest on the p4 is more curved than the condition in *L. leptolophus*, but not sharply inflected as in *L. edwardsi*. Based on these criteria, it is possible to objectively separate out these specimens from the other named species of *Leptoreodon*, so we have given it a new species name, *Leptoreodon golzi*.

DISCUSSION

When we began this project, we were inclined to think that the genus *Leptoreodon* might be taxonomically oversplit, and that examination of large new sample sizes would blur the distinctions between the species. However, as we studied the specimens in detail, we found that most of the diagnoses hold up consistently within fossil samples. Although these distinctions are largely subtle differences in teeth (primarily the p4) (Table 1-2), we are impressed that certain p4 characters

TABLE 1. Comparison of skull measurements of *Leptoreodon* (in mm). Measurements of AMNH 2064 (type of *L. marshi*) and of referred *L. marshi* specimens (types of "*Merycodesmus gracilis*" and "*Camelomeryx longiceps*") after Gazin (1955).

	SDNHM 47878 *L. major*	**AMNH 2064** *L. marshi* (type)	**YPM-PU 11225** "*M. gracilis*"	**YPM-PU 11226** "*C. longiceps*"	**SDNHM 47921** *L. golzi* (type)
C-M3 L	64.1	58.0	64.0	57.5	—
P1-M3 L	54.0	50.8	55.2	51.5	48.7
P1-4 L	34.3	29.5	33.5	31.0	26.2
M1-3 L	23.0	23.0	22.5	21.9	18.2
Canine AP diam/W	6.1/4.0	4.5/—	5.4/3.2	4.5/3.0	3.9/2.0
Canine L	16.1	—	—	—	6.4
P1 L/W	7.1/2.0	4.5/—	5.0/—	3.5/—	4.1/2.5
P2 L/W	8.1/2.5	6.5/—	7.0/—	6.9/2.5	4.9/2.0
P3 L/W	7.5/4.0	7.3/—	7.0/5.0	7.0/6.0	5.8/3.3
P4 L/W	5.4/7.5	6.2/—	5.3/7.0	—/6.5	5.1/4.9
M1	L/W	7.3/9.0	7.0/8.5	6.6/8.9	6.2/7.7 5.1/6.4
M2	L/W	9.0/10.3	8.0/10.0	8.4/10.5	7.3/10.3 5.6/7.5
M3	L/W	8.3/10.2	8.6/11.0	8.9/11.5	8.4/11.6 6.1/7.5
Pmax to occipital condyle	124.5	—	—	—	—
Pmax to lambdoid	139.2	—	—	—	—
Maximum W @ zygoma	52.0	—	—	—	—
Rostral W at canine	23.2	—	—	—	—

TABLE 2. Dental measurements of species of *Leptoreodon* (in mm). Measurements after Gazin (1955), Golz (1976), Kelly (1990), and our own data. N = number of specimens; CV = coefficient of variation; SD = standard deviation; OR = observed range.

L. marshi

	Mean	N	SD	OR	CV
M1-3	22.5	3	0.55	21.9-23.0	2.4
P3 L/W	7.1/5.5	3/2	0.2/0.7	7.0-7.3/5.0-6.0	2.4/12.7
P4 L/W	5.8/6.8	2/2	0.6/0.4	5.3-6.2/6.5-7.0	10.3/5.8
M1 L/W	6.6/8.4	3/3	0.4/0.6	6.2-7.0/7.7-8.9	6.1/7.1
M2 L/W	7.9/10.3	3/3	0.5/0.3	7.3-8.4/10.0-10.5	6.9/2.4
M3 L/W	8.6/11.3	3/3	0.3/0.3	8.4-8.9/11.0-11.6	2.9/2.8
p3 L/W	7.1/2.8	3/2	0.1/0.4	7.0-7.2/2.5-3.0	1.5/1.4
p4 L/W	6.5/3.9	15/15	0.3/0.2	6.1-6.9/3.6-4.6	4.1/6.3
m1 L/W	6.5/5.2	13/13	0.4/0.4	5.8-7.1/4.8-6.1	6.5/7.0
m2 L/W	7.5/6.1	14/14	0.3/0.4	7.0-8.0/5.1-6.8	3.6/7.0
m3 L/W	11.4/6.2	12/12	0.7/0.2	10.3-13.0/5.8-6.5	6.2/3.8

L. major

	Mean	N	SD	OR	CV
M1-3	25.0	2	2.8	23.0-27.0	11.2
P3 L/W	8.0/4.9	2/2	0.6/1.2	7.5-8.4/4.0-5.8	7.5/24.5
P4 L/W	6.2/8.0	2/2	1.1/0.6	5.4-7.0/7.5-8.4	16.1/7.8
M1 L/W	7.8/9.3	2/2	0.6/0.4	7.3-8.2/9.0-9.6	8.1/4.3
M2 L/W	9.2/11.1	3/3	0.2/0.8	9.0-9.3/10.3-11.9	2.1/7.2
M3 L/W	9.0/11.1	2/2	0.9/1.3	8.3-9.6/10.2-12.0	10.0/11.4
p3 L/W	7.5/2.6	1/1	—/—	—/—	—/—
p4 L/W	6.9/3.9	11/11	0.7/0.3	5.9-8.3/3.5-4.8	10.9/8.1
m1 L/W	7.3/5.6	18/18	0.4/0.4	6.6-8.1/5.0-6.5	5.5/7.4
m2 L/W	8.3/6.3	18/18	0.7/0.5	6.7-9.5/5.3-7.3	8.4/8.0
m3 L/W	12.2/6.4	13/13	0.9/0.5	10.4-13.5/5.6-7.2	7.6/8.1

L. pusillus

	Mean	N	SD	OR	CV
M1-3	—	0	—	—	—
P3 L/W	5.5/4.0	1/1	—/—	—/—	—/—
P4 L/W	5.1/4.8	1/1	—/—	—/—	—/—
M1 L/W	5.5/6.7	2/2	0.1/0.1	5.4-5.6/6.6-6.7	1.8/0.01
M2 L/W	5.9/7.6	3/3	0.4/0.3	5.4-6.3/7.3-7.8	6.7/3.3
M3 L/W	6.3/7.9	2/2	0.2/0.07	6.1-6.4/7.8-7.9	3.1/0.8
p3 L/W	4.6/1.8	1/1	—/—	—/—	—/—
p4 L/W	4.9/2.5	1/1	—/—	—/—	—/—
m1 L/W	5.2/3.8	1/1	—/—	—/—	—/—
m2 L/W	5.3/4.1	1/1	—/—	—/—	—/—
m3 L/W	8.2/4.8	1/1	—/—	—/—	—/—

L. edwardsi

	Mean	N	SD	OR	CV
M1-3	19.7	2	0.6	19.2-20.1	3.0
P3 L/W	6.3/3.7	3/3	0.2/0.3	6.1-6.5/3.4-4.0	3.2/8.1
P4 L/W	5.3/6.0	10/10	0.4/0..3	4.5-5.9/5.6-6.5	8.1/4.7
M1 L/W	6.4/7.9	10/10	0.2/0.3	6.0-6.7/7.5-8.6	3.6/4.3
M2 L/W	6.8/8.8	10/10	0.4/0.5	6.3-7.6/8.0-9.7	6.3/5.6
M3 L/W	7.3/9.3	10/10	0.3/0.4	6.9-8.0/8.5-9.8	4.3/4.3
p3 L/W	6.4/2.6	10/10	0.2/0.2	6.0-6.6/2.3-2.9	3.2/8.5
p4 L/W	6.2/3.4	20/20	0.3/0.2	5.6-6.7/3.1-3.7	4.4/5.0
m1 L/W	6.1/5.0	20/20	0.3/0.3	5.7-6.8/4.4-5.6	4.4/6.2
m2 L/W	6.9/5.7	20/20	0.3/0.3	6.6-7.6/5.2-6.2	3.8/4.7
m3 L/W	10.4/5.8	20/20	0.3/0.3	10.0-10.8/5.3-6.6	2.5/5.5

L. leptolophus

	Mean	N	SD	OR	CV
M1-3	20.1	7	0.4	19.4-21.0	1.9
P3 L/W	5.9/2.4	4/4	0.3/0.4	5.7-6.1/2.2-2.5	5.1/1.7
P4 L/W	5.1/6.0	6/6	0.4/0.2	4.9-5.3/5.7-6.4	7.8/3.3
M1 L/W	6.3/7.4	12/12	0.3/0.2	5.9-6.8/7.2-7.7	4.8/2.6
M2 L/W	7.1/8.5	15/15	0.2/0.3	6.6-7.5/7.9-8.9	3.4/3.8
M3 L/W	7.3/8.7	12/12	0.4/0.5	6.5-8.0/7.9-10.0	5.3/5.9
p3 L/W	6.1/2.3	5/5	0.4/0.2	6.0-6.3/1.7-2.7	6.6/8.7
p4 L/W	6.4/3.3	4/4	0.3/0.2	6.2-6.6/3.2-3.3	4.7/6.1
m1 L/W	6.4/4.5	14/14	0.3/0.5	6.0-6.9/3.3-5.4	4.1/12.0
m2 L/W	7.3/5.1	10/10	0.4/0.5	6.6-7.8/4.2-5.6	4.8/9.6
m3 L/W	10.5/5.0	6/6	0.4/0.6	10.0-11.1/4.5-5.7	3.4/11.7

L. golzi

	Mean	N	SD	OR	CV
M1-3	18.2	1	—/—	—/—	—/—
P3 L/W	5.8/3.3	1	—/—	—/—	—/—
P4 L/W	5.1/4.9	1	—/—	—/—	—/—
M1 L/W	5.1/6.4	1	—/—	—/—	—/—
M2 L/W	5.6/7.5	1	—/—	—/—	—/—
M3 L/W	6.1/7.5	1	—/—	—/—	—/—
p3 L/W	5.4/2.1	1	—/—	—/—	—/—
p4 L/W	5.1/2.8	36/36	0.4/0.2	4.4-6.4/2.3-3.3	8.1/8.4
m1 L/W	5.4/4.2	33/33	0.5/0.3	4.6-6.4/3.6-4.9	8.9/7.0
m2 L/W	6.0/5.0	31/31	0.6/0.3	5.1-7.1/4.5-5.6	9.5/5.8
m3 L/W	9.2/5.1	22/22	0.6/0.3	8.3-10.9/4.7-5.6	6.9-5.3

L. stocki

	Mean	N	SD	OR	CV
P3 L/W	7.2/4.6	1/1	—/—	—/—	—/—
P4 L/W	5.7/6.2	3/3	0.3/0.2	5.2-5.8/6.0-6.2	4.7-3.4
M1 L/W	7.1/8.8	2/3	0.07/0.5	7.0-7.1/8.2-9.1	1.0/5.6
M2 L/W	7.7/9.9	2/2	0.3/—	7.5-7.9/—	3.6/—
M3 L/W	8.3/10.5	4/4	0.1/0.4	8.2-8.4/10.0-10.8	1.1/3.4
p3 L/W	6.3/3.1	5/3	0.4/0.1	5.7-6.8/3.0-3.2	5.9/4.3
p4 L/W	6.6/3.6	14/14	0.5/0.2	5.6-7.4/3.2-4.0	8.1/6.5
m1 L/W	6.4/5.1	22/22	0.5/0.4	5.0=7.2/4.4-5.8	7.6/7.1
m2 L/W	7.5/5.9	19/19	0.7/0.4	6.3-8.7/5.1-6.6	8.8/6.9
m3 L/W	11.0/6.0	16/16	0.7/0.3	9.2-11.7/5.5-6.5	6.7/5.2

are consistent within populations (such as the distinction between *L. edwardsi* and *L. leptolophus*), and that those population samples do not overlap geographically (e.g., *L. edwardsi* is restricted to the late Uintan of the Sespe Formation and Texas; *L. leptolophus* to the late Uintan of San Diego County and the Duchesnean of Texas). The fact that these taxa were erected by recent workers (e.g., Golz, 1976) who were not inclined to oversplitting is further confirmation of their validity. This has been verified by independent workers (e.g., Wilson, 1984; Westgate, 1990) when they examined new samples of *Leptoreodon* from different regions. Some may question the biological significance of so many similar-sized small artiodactyls differentiated only by subtle differences in teeth whose functional differences are unknown, and we cannot com-

pletely explain this phenomenon either. However, the primitive artiodactyls of the Eocene are well known for being highly speciose (e.g., Stucky, 1998), and apparently subdivided the ecological niches in the dense jungles of the middle Eocene as the many sympatric and similar-sized duiker antelopes do in Africa today.

Sexual dimorphism can be ruled out as a cause for this variability in the samples. For one thing, Golz (1976, Table 23) showed that where large samples of a single population with multiple canines exist (as in the sample of *L. edwardsi*, which had 12 presumed male and 9 presumed female canines), they are disjunctly different in size, yet the condition of the cheek teeth is consistent within the population. Second, each cheek-tooth morphology is restricted to one or two geographic regions, and no two similar-sized species occur in the same region; of these samples, several (such as *L. edwardsi*) clearly have both presumed male and female canines associated with similar cheek teeth. Thus, the simplest conclusion is that they are valid species, each with some sexual dimorphism in the upper canines, but not in any other known characteristic.

The geographic patterns of each species of *Leptoreodon* are shown in Figure 11. This is a marked contrast to the earlier, more limited distribution of *Leptoreodon* as suggested by Golz (1976) based on material known 25 years ago.

CONCLUSIONS

Large new collections of the primitive hornless protoceratid *Leptoreodon* show that there were at least seven distinct species (one new) found in the middle (early Uintan to early Duchesnean) Eocene of California, Texas, Utah, Wyoming, Montana, and Saskatchewan (Fig. 11). The larger species *L. marshi* and *L. major* are found in the early Uintan of California, Utah, west Texas, and Saskatchewan, together with the diminutive *L. pusillus* in West Texas. By the late Uintan, all seven species were present: *L. marshi* is still found in Montana, *L. major* in west Texas, *L. pusillus* in San Diego and the Texas Gulf Coastal Plain. Several other species were added: the highly derived *L. edwardsi* in the Sespe Formaton and in West Texas; the sharp-crested *L. leptolophus* in San Diego and the Texas Gulf Coast; the larger *L. stocki* in the Sespe Formation, and the smaller new species, *L. golzi*, in San Diego County. In the early Duchesnean, *L. marshi* persists in west Texas, as does *L. pusillus* and *L. leptolophus* (which are also known from the Duchesnean of San Diego County). *L. stocki* persists into the Duchesnean in the Sespe Formation.

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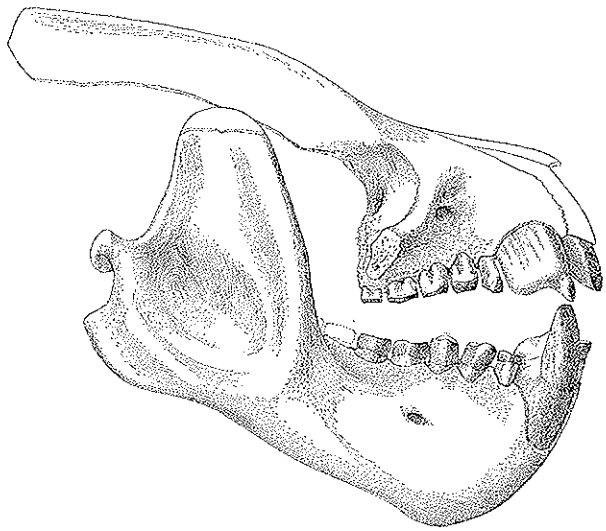

Psittacotherium multifragum, part of skull and lower jaw (from Matthew, 1937).