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Prodiacodon crustulum (Leptictidae, Mammalia) from the Tullock Member of the Fort Union Formation, Garfield and McCone Counties, Montana, USA

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Since Michael J. Novacek (1977) established *Prodiacodon crustulum,* the hypodigm of this species has been greatly increased. Currently, over 100 isolated teeth, but only a single dentulous fragment of a dentary, are known. Reconstruction of its dentition has been based on comparisons with the more completely represented dentition of *P. puercensis* Matthew, 1929, from younger Torrejonian 1-3 North American Land Mammal Age (NALMA) local faunas of the San Juan Basin, New Mexico. *Prodiacodon crustulum* is known from the Puercan 3 (NALMA) Garbani Channel and, possibly, Purgatory Hill local faunas in Montana. It differs from *P. puercensis* in the smaller size of its postcanine dentition and lesser development of minor cusps on the upper and lower molars. Given the uncertainties in reconstruction of its dentition, the new sample adds little toward illustrating the phylogenetic relationships of the species to more recent Paleogene and Neogene leptictids. Recent studies support recognition of the clade Leptictida McKenna, 1975, including the leptictids and the Cretaceous species of *Gypsonictops* Simpson, 1927. More data are needed to test the hypothesis that *P. crustulum* is the earliest known representative of the Afrotheria Stanhope et al., 1998.

Keywords: *Prodiacodon*, Leptictidae, Mammalia, Tullock Member, Puercan, Montana

INTRODUCTION

In an earlier review of Paleocene and Eocene leptictids, Novacek (1977) established the species *Prodiacodon crustulum* Novacek. The hypodigm of the species consisted of a small number, 23, of isolated upper and lower postcanines from Biscuit Springs (University of California Museum of Paleontology Locality V74122) and other approximately contemporaneous localities in the Tullock Member of the Fort Union Formation. These sites yield samples of the Garbani Channel fauna, now referable to the Puercan 3, North American Land Mammal Age (Clemens 2013, Sprain et al. 2014). Since 1977 the sample of *P. crustulum* has been significantly expanded to over 100 complete and fragmentary isolated teeth, but includes only one fragment of a dentary, which preserves p2, a fragment of p4, and p5. Identifications of other elements of the premolar and molar dentitions are based primarily on comparisons with the published record of the Torrejonian leptictid *P. puercensis* Matthew, 1918, (see also Matthew 1929, 1937, Novacek 1977, 1986), which includes descriptions of much more complete fossils documenting the composition of its postcanine dentition.

As part of an ongoing analysis of the composition of the Garbani Channel fauna, the goals of this study are to describe the fragmentary dentary and isolated teeth now referred to *P. crustulum*; document the current fossil record of leptictids in the Tullock Member of the Fort Union Formation in Garfield and McCone counties, Montana; and survey what is known of the evolution of the Leptictida (Novacek 1986) during the Puercan and early Torrejonian. Because the reconstruction of the dentition of *P. crustulum* has had to be based substantially on detailed comparisons with the dentition of *P. puercensis*, no attempt has been made to reevaluate Novacek's (1977) or later hypotheses concerning the phylogenetic interrelationships of the species of *Prodiacodon* Matthew, 1929, or their phylogenetic relationship to the various later genera of leptictids and other eutherians.

MATERIALS AND METHODS

Dental terminology

Individual teeth—Premolars are identified as P/p, molars as M/m, and deciduous premolars as DP/dp. Upper postcanine teeth are identified with a capital letter (e.g., P4) and lower teeth with a lower case letter (e.g., p4). Criteria have not been found to differentiate between both isolated upper first and second molars and lower first and second molars of *Prodiacodon crustulum*. These teeth are designated M1-2 and m1-2, respectively, to recognize the lack of characters to differentiate these isolated teeth.

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Dental formula—In recent studies of the Leptictida, two systems for identifying the positions of premolars have been adopted. One stems from the hypothesis of a close phylogenetic relationship between leptictids and the Cretaceous genus *Gypsonictops* Simpson, 1927, which had five lower premolars (Lillegraven 1969, Clemens 1973) and four or possibly five upper premolars (Fox 1977). McKenna (1975) argued that the most primitive eutherians had five upper and five lower premolars and that the third premolars were lost in the course of evolution of the group. Consequently, he designated the remaining premolars of leptictids as P/p1, P/p2, P/p4, and P/p5. Novacek (1977) adopted this formula, and recently this interpretation received support from a study of eutherian evolution by O'Leary et al. (2013).

In contrast, Cifelli (2000) noted that in many studies the P/p4s and P/p5s of leptictids were interpreted as homologs of teeth designated P/p3 and P/p4 in the dentitions of other eutherians. He recommended that in eutherians with five premolariforms these teeth be identified as P/p1, P/p2, P/pX, P/p3, and P/p4. Similar alternative systems of identification of the five premolariforms had been suggested (Lillegraven 1969, Clemens 1973, Kielan-Jaworowska 1981). Identification of the premolars of leptictids as P/p1 through P/p4 has been used by several authors, for example, Gunnell et al. (2008) in their review of Paleogene and Neogene leptictids and in the description of a new leptictid, *Megaleptictis* Meehan and Martin, 2012.

Here the isolated teeth available to Novacek (1977) and the new sample of *P. crustulum* are described and analyzed. To facilitate integration with Novacek's study, the premolars of *P. crustulum* are identified as P/p1, P/p2, P/p4, and P/p5. Dental measurements were taken according to the criteria illustrated by Novacek (1977, fig. 2). Images in Figures 3 through 8 illustrate epoxy casts of the teeth.

Stratigraphy

The Garbani Channel filling is a unit within the Tullock Member of the Fort Union Formation (Archibald 1982). The rank of the Tullock has varied from recognition as a distinct formation to classification as a member of the Fort Union Formation. The latter classification, currently favored by the United States Geological Survey, is followed here.

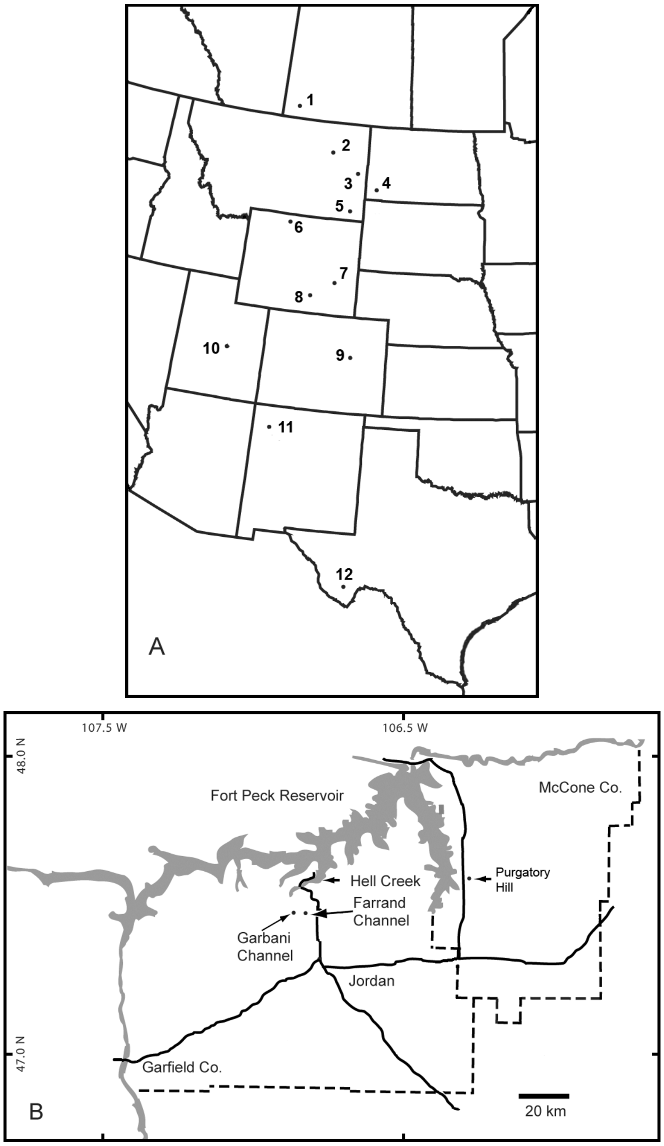

Figure 1A, B. Locality maps. **A.** Fossil localities and local faunas in the North American Western Interior cited in the text. **1.** Saskatchewan, Canada, Long Fall, Frenchman 1, Rav W-1, and Croc Pot. **2.** Localities in Garfield and McCone counties, Montana, see Fig. 1B. **3.** Hiatt local fauna, Makoshika State Park, Montana. **4.** PITA Flats local fauna, North Dakota. **5.** Spigot-Bottle local fauna, Montana. **6.** Mantua Lentil local fauna, Wyoming. **7.** Lance Formation, Wyoming. **8.** Ferris Formation, Wyoming. **9.** Littleton locality, Denver Basin, Colorado. **10.** Wagonroad and Dragon local faunas, Utah. **11.** San Juan Basin, New Mexico. **12.** Big Bend, Texas. **B.** Localities in Garfield and McCone counties, Montana.

In Garfield and McCone counties, northeastern Montana (Fig. 1), the Tullock Member has yielded local faunas of Puercan (Pu) and earliest Torrejonian (To) ages (Clemens and Wilson 2009, Clemens 2013, Sprain et al. 2014). The Puercan NALMA is divided into three interval zones (Lofgren et al. 2004). Currently recognized local faunas in the Tullock Member are assigned to the Pu1, Pu3, and To1 interval zones. Local faunas representing the Pu2 interval zone have yet to be discovered and described. New high resolution ^{40}Ar/^{39}Ar age determinations indicate that the Pu1 interval zone encompasses at least approximately the first 70 kyr of the Paleocene (Sprain et al. 2014). The duration of the Pu3 interval zone cannot be as precisely constrained, but it appears to have fallen in an interval between approximately 300 and 900 kyr after the Cretaceous/Paleogene boundary. Torrejonian local faunas from Garfield County cited here are assigned to the To1 interval zone and existed sometime during the following approximately 70 kyr.

Institutional abbreviations

AMNH, American Museum of Natural History, **LACM**, Natural History Museum of Los Angeles County; **UCMP**, University of California Museum of Paleontology.

SYSTEMATIC PALEONTOLOGY

LEPTICTIDA McKenna, 1975
LEPTICTIDAE Gill, 1872
Prodiacodon Matthew, 1929
Prodiacodon crustulum Novacek, 1977
Figs. 2–8

Holotype—UCMP 114990, UCMP loc. V74122, left upper molar (M1 or M2).

Revised diagnosis—Postcanines are smaller than those of *Prodiacodon puercensis*. Differing from *P. puercensis*, upper molars of *P. crustulum* have relatively wider stylar shelves, variable presence of a small stylocone, smaller hypocones, shorter and smaller (in basal dimensions) metacones relative to paracones. Also, the paraconule and smaller metaconule are well developed and situated on the pre- and postprotocrista closer to the apex of the protocone than to the bases of the paracone and metacone. Differing from the type and paratype of *P. puercensis,* on only a few upper molars a small cuspule is present anterolabial to the paraconule. In both species, on P5 and the upper molars the precingulum is crenulated by series of folds and/or cuspules as is the transversely longer postcingulum. Unlike *P. puercensis*, in which it is salient, the mesial end of the crown of p5 is blunt with a small cusp present lingual to the paraconid. Talonids of m1 and m2 differ from those of the paratype of *P. puercensis* in usually having only three cusps; the majority lacks an entoconulid. An entoconulid is present on the talonids of most m3s.

Hypodigm—Other than a fragment of a dentary with p2, a fragment of p4 and p5, UCMP 224048, the hypodigm consists of isolated teeth (Table 1). Identification of the positions of the isolated teeth in the dentition has been based primarily on comparisons with the paratype of *P. puercensis* (Novacek 1977, fig. 8; 1986, fig. 4; Matthew 1918, figs. 6-9; 1937, plate 55, figs. 1-8) and more recent leptictids. Dimensions of the postcanines are given in Table 2.

Description

Dentary, p2, p4, and p5—A right dentary (UCMP 224048, Fig. 2) preserves p2, a fragment of p4, and p5. The p2 has a single central cusp (protoconid). A crest extends mesially from the protoconid to a miniscule cusp

Table 1. Hypodigm of *Prodiacodon crustulum*. UCMP locality numbers in bold font; UCMP (lacking acronym) and LACM specimen catalog numbers in regular font. *Specimens available for Novacek's (1977) study.

p 5:	**V73080**, 186622, 224048; **V73082**, 192149; **V74119**, 224052; **V74122**, *114978; V**74123**, *114993.
?dp 5:	**V73080**, 224050; **V73082**, 192148, 218894; **V74120**, 224051; **V75193**, 218895.
m 1-2:	**V72125**, 192072; **V72128**, 192073-192075; **V72129**, 192076-192080; **V72134**, 224055; **V73080**, 186604, 186643, 189420, 192081-192090, 224053; **V73082**, 192091, 192093; **V73096**, 110534, 224054; **V74119**, 192095; **V74122**, *114981, *114986, 192096-192099; **V74123**, *114991, *114992, **V74127**, 192103; **V75193**, 192101, 192102, 218896; **V99438**, 192094, 192104, 192095, 192107-192110, 218897, 218898, 224056, 224057.
m 3:	**V72131**, 224058; **V74112**, *114985; **V75193,** 224061; **V75194**, 224062; **V78082**, 189518; **V73080**, 224059, 224060; **V99438**, 218899, 224063.
P 4:	**V74122**, *114974, *114979; **V99438**, 224084.
P 5:	**V73080**, 192144, 224086; **V74122**, *114972, 224078, 224082; **V99438**, 224083.
M 1-2:	**V72126**, 224064; **V72128**, 224065; **V72130**, 224066; **V72134**, *LACM 32970; **V73080**, 223175, 224067-8, 224071, 224089; **V74122**, *114973, *114975-114977, *114980, 114990; **V75194**, 224072; **V75195**, 192146; **V99438**, 192145, 224073-7.
M 3:	**V72129**, 224079; **V72137**, 192147; **V73080**, 224085; **V99438**, 224081.

Table 2. Dimensions of postcanines of *Prodiacodon crustulum*. All dimensions in millimeters. N = number, OR = observed range.

Element	**N**	**Length**	**Width**				
p 2	1	2.36	1.40				
		OR length	**Mean**	**OR width trigonid**	**Mean**	**OR width talonid**	**Mean**
p 5	7	3.25-3.45	3.33	1.46-1.80	1.58	1.44-1.56	1.48
m 1-2	53	1.93-3.14	2.69	1.22-2.44	1.95	1.06-2.01	1.63
m 3	8	2.54-3.40	3.08	1.58-2.14	1.86	1.25-1.70	1.46
		OR length	**Mean**	**OR mesial width**	**Mean**	**OR distal width**	**Mean**
P 4	3	3.06-3.25	3.16	2.09-2.20	2.14	2.11-2.38	2.27
P 5	6	2.31-2.53	2.42	2.93-3.03	2.98	3.01-3.40	3.22
M 1-2	21	2.35-2.86	2.59	3.25-3.96	3.63	3.57-4.12	3.83
M 3	5	2.04-2.54	2.11	3.50-4.21	3.80		

at the base of the crown. Another crest on the distal slope of the protoconid extends to a shallow basal pocket. The length of the crown of p2 is distinctly smaller than that of p5. The mesial end of the crown of p4 is missing. On its distal slope, two ridges end in a shallow talonid-like depression. All three premolars were supported by two roots. An X-ray of the dentary (Fig. 2C) reveals that the roots of p5 are essentially parallel indicating it probably is a permanent premolar.

Clemens and Wilson (2009) recognized the presence of *Prodiacodon* cf. *P. crustulum* at the Two Mosquitoes locality (UCMP loc. V76171), Torrejonian 1, in the Farrand

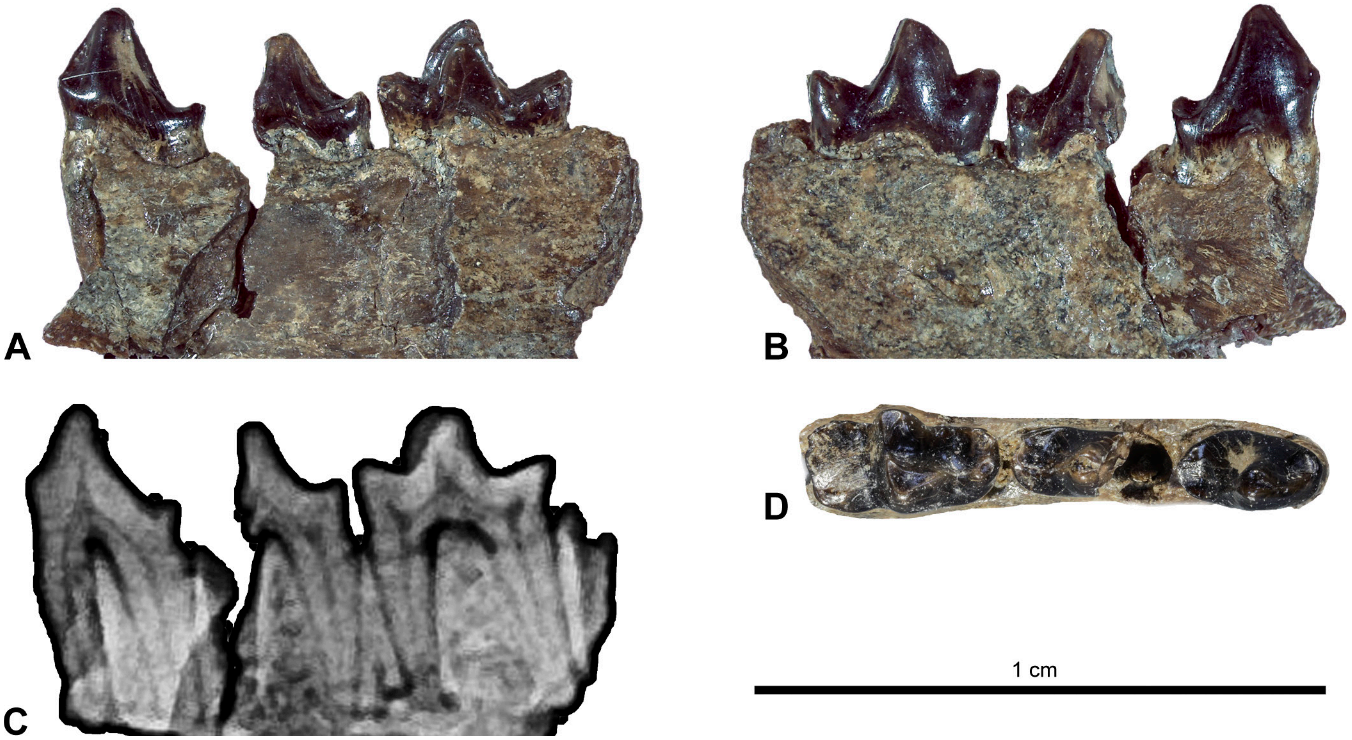

Figure 2A–D. Right dentary of *Prodiacodon crustulum* with p2, fragment of p4, and p5, UCMP 224048. **A.** Lingual view. **B.** Labial view. **C.** X-ray, lingual view. **D.** Occlusal view.

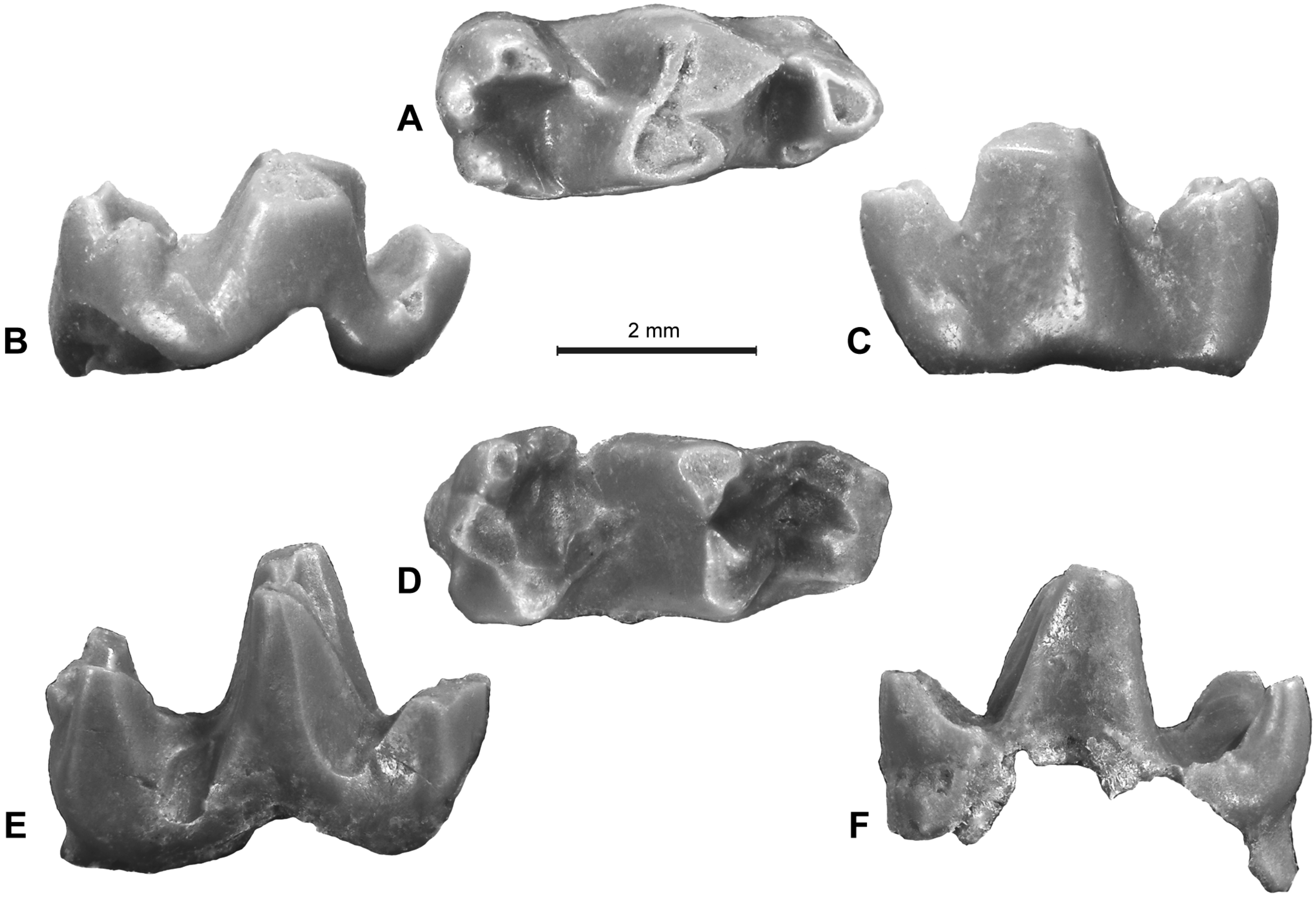

Figure 3A–F. Lower premolars of *Prodiacodon crustulum*. UCMP 192148, left ?dp5. **A.** Occlusal view. **B.** Lingual view. **C.** Labial view. UCMP 192149, right p5. **D.** Occlusal view. **E.** Labial view. **F.** lingual view.

Channel, Garfield County. The sample includes a fragment of a dentary with the distal wall of the distal alveolus of p4, alveoli of the two-rooted p5, m1, and m2 (UCMP 189532). Resembling the type of *P. puercensis*, the estimated length of p5 is greater than that of m1. The same difference in length of crown characterizes the isolated p5s and m1-2s of *P. crustulum*.

p5—The paraconid is directly mesial to the protoconid and connected to it by a low paralophid (Fig. 3D–F). A cusp lingual to paraconid produces a relatively broad, blunt mesial end of the crown. The large, trough-like trigonid basin opens between the cusp lingual to the paraconid and metaconid. The protoconid is of greater volume and slightly taller than the metaconid, which is set slightly distal to the protoconid. In occlusal view, the talonid is shorter, mesio-distally, than the trigonid. The three primary talonid cusps are aligned labiolingually. The cristid obliqua is not prominent and heavily worn on the available specimens. An entoconulid is present on one of the two p5s that preserve this area. All p5s were supported by two roots. The p5 figured by Novacek (1977, fig. 13A, B, UCMP 114982) is a heavily abraded tooth and not representative of the morphology of the other, less damaged teeth recognized here as p5s of this species.

?dp5—With the exception of the morphology of the mesial end of the crown, in most respects three isolated teeth resemble the p5s referred to *P. crustulum* (Fig. 3A–C). Unlike the teeth identified as p5s, the paraconid lacks or has only a miniscule cusp lingual to it. As a result, the mesial end of the crown is salient and not laterally expanded. In comparison to the teeth identified as p5s, the crowns are slightly longer and narrower. What remains of the two roots of these specimens suggests they were relatively widely separated. Identification of these teeth as deciduous premolars *P. crustulum* is tentative.

m1-2—Novacek's (1977) sample of m1s and m2s consisted of only five isolated teeth. UCMP 114986 (loc. V74122) was figured (Novacek 1977, fig. 13C, D) and tentatively identified it as an m2. With the exception of an m3, he did not identify the positions of the other molars in the dental arcade. The sample has been expanded to a total of 53 isolated molars that are either m1s or m2s. Consistent criteria for distinguishing these two molars have not been discovered, and they are identified as m1-2s.

On m1-2 (Figs. 4, 5A–C) the paraconid is the smallest trigonid cusp and is connected to the protoconid by a distinct paralophid. With wear, the segment of the paralophid on the labial slope of the paraconid tends to form a blade-like structure. A short basal cingulid is present below the paralophid at the mesiolabial corner of the crown. The apex of the paraconid is slightly labial to that of the metaconid. These cusps tend to be closely approximated, but the degree of separation varies. The metaconid is slightly distal to the protoconid. The trigonid is distinctly higher than the talonid.

Lingually, the talonid basin tends to be deeply open. Of the three major cusps ringing the talonid basin the hypoconid usually is the highest. The hypoconulid is central at the distal end of the basin, and the entoconid is set slightly mesial to hypoconulid. Novacek (1977) noted that the m1 and m2 of *P. crustulum* differed from those of *P. puercensis* in the absence of an entoconulid. This is the case on the four m1s or m2s available for his study. The current larger sample documents variation in this character. Of the 38 unworn or partially worn teeth preserving the morphology of this part of the talonid basin an entoconulid is present on 14. Where present, usually the entoconulid is a minute cusp. On one tooth, two minute cusps are present in this position. Variation in the development of a mesoconid on the cristid obliqua, approximately midway between the apex of the hypoconid and the back of the trigonid, is documented in the larger sample. Of the 30 unworn or partially worn teeth preserving the top of this crest a slight expansion or a distinct cusp is present on 14. Of these only three have both an entoconulid and a mesoconid.

m3—In the positions of the trigonid cusps and their relative sizes the m3s (Fig. 5D–F) do not differ from those of m1-2s. In contrast, the talonids of the m3s are relatively longer, primarily reflecting the large, conical hypoconulid that extends farther distally than the hypoconulids of the other lower molars. Widths of the talonids are smaller than those of the trigonids. Labiolingually the entoconid and slightly smaller hypoconid are positioned opposite one another. Only one m3 (UCMP 114985) was present in the sample available to Novacek (1977, Fig. 13E, F). He noted in the diagnosis of the species that a small entoconulid was present. Of the six m3s in the current sample three have very small entoconulids. A mesoconid is present on

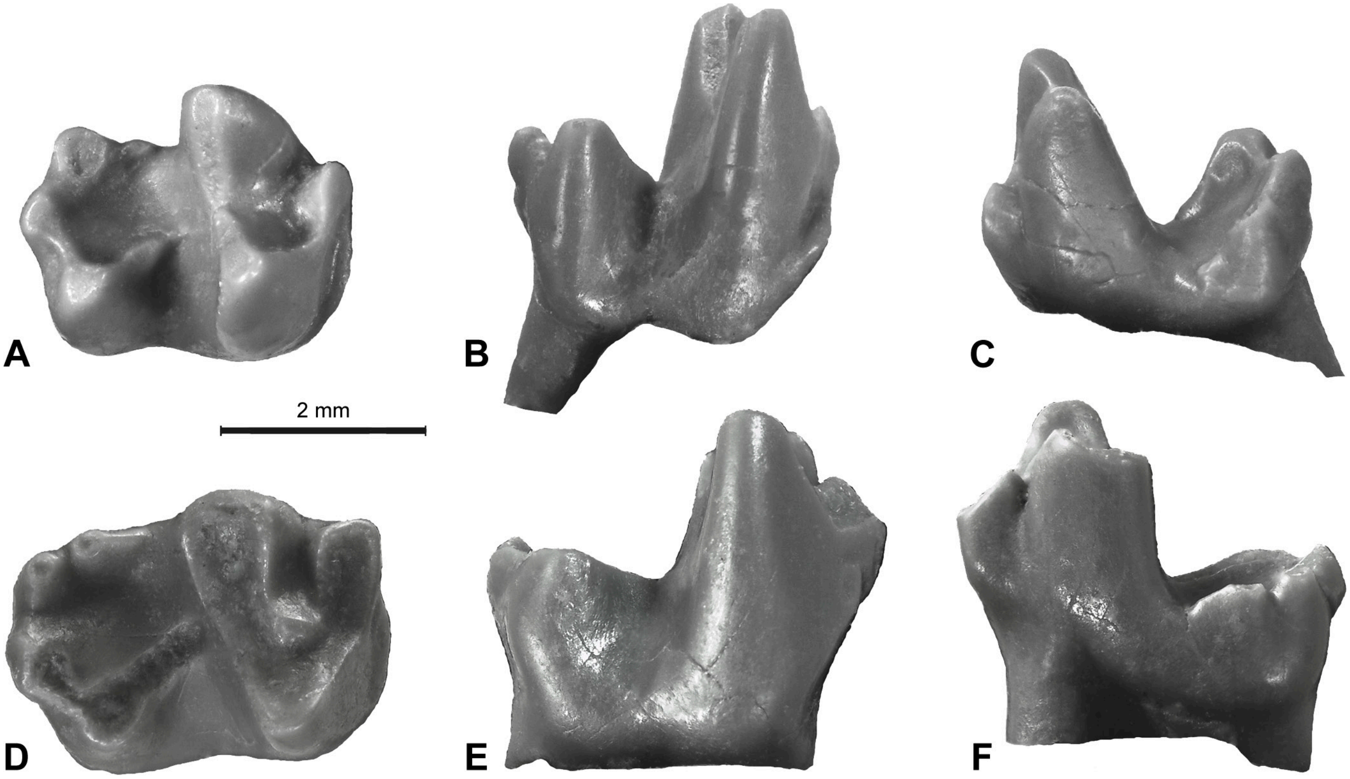

Figure 4A–F. Lower molars of *Prodiacodon crustulum*. UCMP 110534, right m1-2. **A.** Occlusal view. **B.** Labial view. **C.** Lingual view. UCMP 192091, right m1-2. **D.** Occlusal view. **E.** Labial view. **F.** Lingual view.

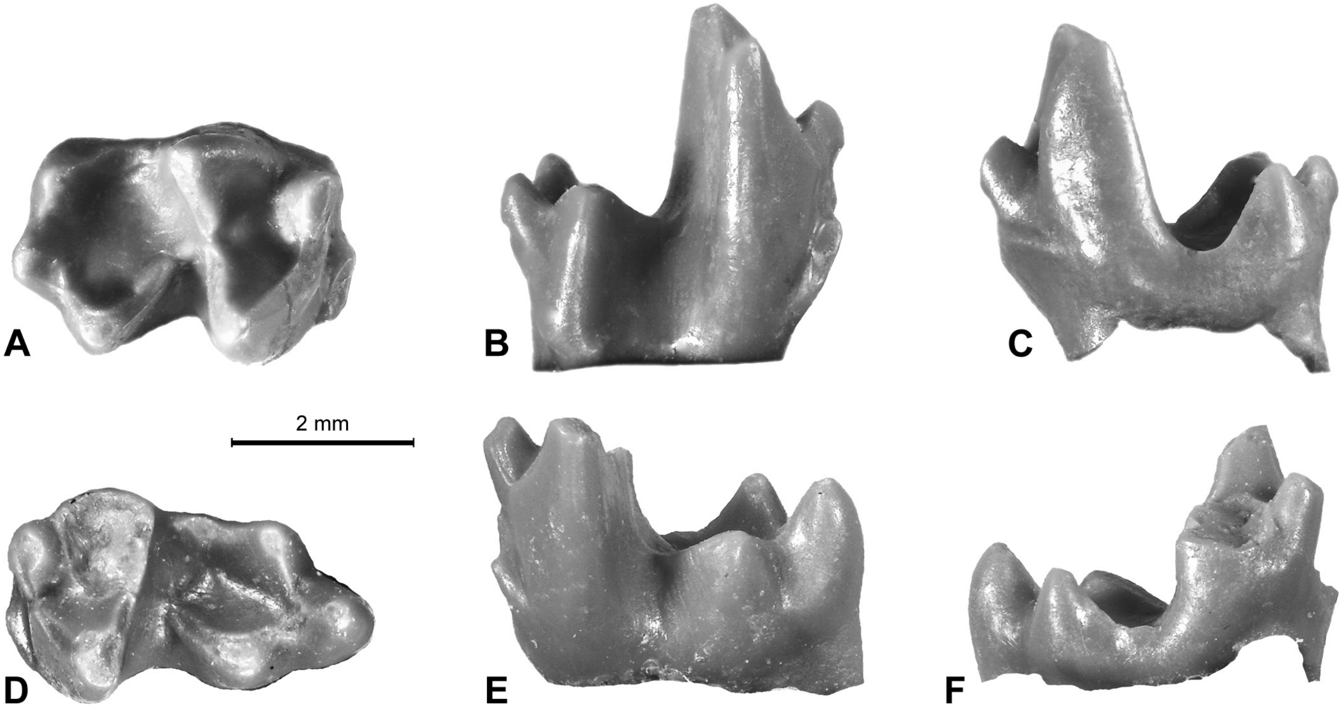

Figure 5A–F. Lower molars of *Prodiacodon crustulum*. UCMP 114986, right m1-2. **A.** Occlusal view. **B.** Labial view. **C.** Lingual view. UCMP 114985, left m3. **D.** Occlusal view. **E.** Labial view. **F.** Lingual view.

the cristid obliqua of three of the m3s.

P4—The largest cusp of the crown is the paracone; the metacone is distinctly smaller (Fig. 6A–C). This difference in size is greater than that on P5 and M1-2. A crest extending mesially from the paracone to the tip of the salient but broad parastyle divides its occlusal surface into labial and lingual basins. The narrow ectocingulum extends from the labial slope of the paracone to the distolabial corner of the crown. A narrow crest extends from this corner of the crown across the distal side of the metacone. The protocone is a simple, lingually directed cusp. Neither a trigon basin nor conules are present. Three roots supported the crown.

P5—The crowns of the P5s resemble those of M1-2s in being mesio-distally short relative to the transverse width (Fig. 6D–F), but differ in their somewhat smaller size. In occlusal view, the ectocingulum has a straight or slightly indented labial margin and tends to be narrow, lacking or with only a few minor cusps. Relative positions of the paracone, metacone, and conules are like those of M1-2s. The paraconule is larger and rises higher above the trigon basin than the metaconule. Only one paraconule is present on the P5s. In comparison to the molars, the pre- and postcingula are narrower, shorter transversely, and not as crenulated. A distinct hypocone is not present. The crown was supported by three roots.

M1-2—The crowns of these isolated molars are elongated transversely relative to their mesio-distal length and have sharp piercing cusps (Figs. 7, 8A–D). In occlusal view, on a majority of the teeth the ectocingulum has a straight labial margin, but on some there is a relatively shallow ectoflexus. The parastylar region is salient. A crest on the labial side of the ectocingulum bears small irregular cuspules from approximately the middle of the crown to its distal end. Rarely there is a faint indication of a stylocone.

The paracone is slightly larger in basal diameter and higher than the metacone. Para- and metaconules are set lingually with the paraconule closer to the protocone, not at the bases of the paracone and metacone as in *Palaeictops* **Matthew, 1899**, and *Leptictis* **Leidy, 1868**. The crest from the protocone to the paraconule extends labially to form a paracingulum across the mesial base of the paracone. This crest is consistently larger and higher than the crest that extends from the protocone to the metaconule and on to join the metacingulum across the distal side of the metacone. In mesio-distal cross section this difference in height produces an asymmetrical trigon basin.

Of the three M1s or M2s available for **Novacek's (1977)** study, one (LACM 32970, Fig. 7A–D) has the "doubled" paraconules cited by Novacek. On another (UCMP 114990, the holotype) the crest of the paraconule ridge is slightly expanded labial to the paraconule. On the third

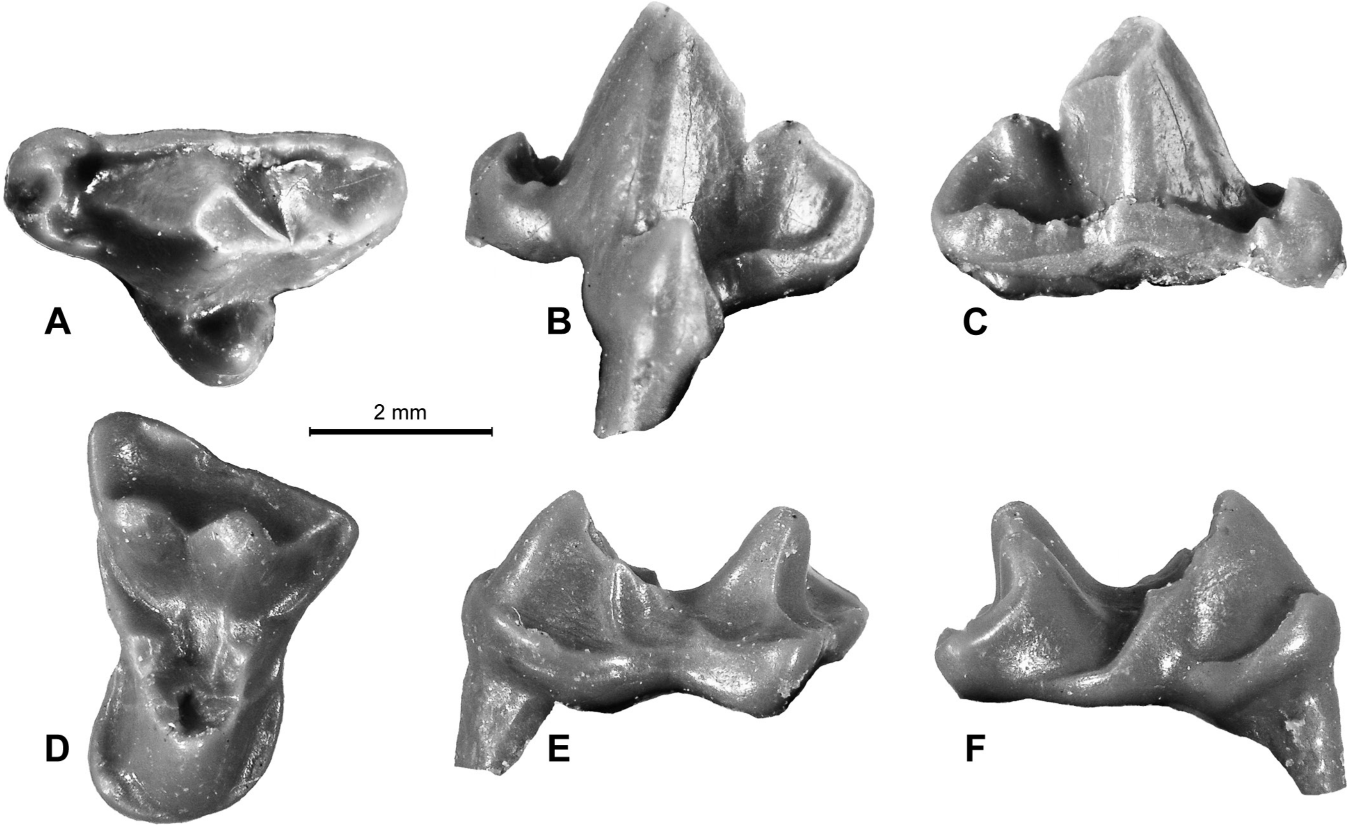

Figure 6A–F. Upper premolars of *Prodiacodon crustulum*. UCMP 114979, left P4. **A.** Occlusal view. **B.** Lingual view. **C.** Labial view. UCMP 192144, right P5. **D.** Occlusal view. **E.** Mesial view. **F.** Distal view.

(UCMP 114976) a slight indentation suggests subdivision of the ridge. Subsequently, 12 teeth identified as M1-2s with the paraconule region preserved have been discovered. Of these, five resemble the holotype (e.g., UCMP 192146, Fig. 7E–H) in a slight indication of doubling of the paraconule; the others have single paraconules (e.g., UCMP 192145, Fig. 8A–D). On one of these teeth (UCMP 224077) two small cusps are present in the region of the metaconule.

Precingula nearly reach the anterolabial corner of the crown. Lingually they usually end labial to the lingual slope of the protocone. The precingula are variable in height and width. The postcingula are larger and noticeably more expanded posterolingually. On only one tooth (UCMP 224076) do the pre- and postcingula meet across the lingual side of the protocone. Of the nine teeth with unworn postcingula, four have a small, short but distinct hypocone.

M3—Unlike the M1-2s, the weak paracrista extends from the paracone to the parastyle and not to a minute stylocone when one is present (Fig. 8E–H). The ectocingulum narrows distally ending at the mesial face of the metacone. The precingulum and, particularly, the postcingulum are smaller than those of the preceding molars. Resembling the M1-2s the paracone is slightly higher than the metacone. The more lingually positioned paraconule is higher than the metaconule. Of the two specimens on which this region is preserved, one has a doubled paraconule, the other a single paraconule.

STRATIGRAPHIC AND BIOGEOGRAPHIC DISTRIBUTIONS

The vast majority of fossil localities yielding records of the latest Cretaceous and early Paleogene terrestrial biotas are in the North American Western Interior, an area generally to the east of the Rocky Mountains extending from Alberta and Saskatchewan to the Big Bend area of Texas (Fig. 1A). Records of the occurrences of leptictidans—members of the Gypsonictopidae Van Valen, 1967 and Leptictidae—within this area are relatively rare and geographically irregular in distribution, particularly during the Puercan NALMA.

Lancian records

Gypsonictops hypoconus Simpson, 1927 and *G. illuminatus* Lillegraven, 1969 are commonly represented in Lancian NALMA local faunas in northeastern Montana and other areas of the Western Interior extending from

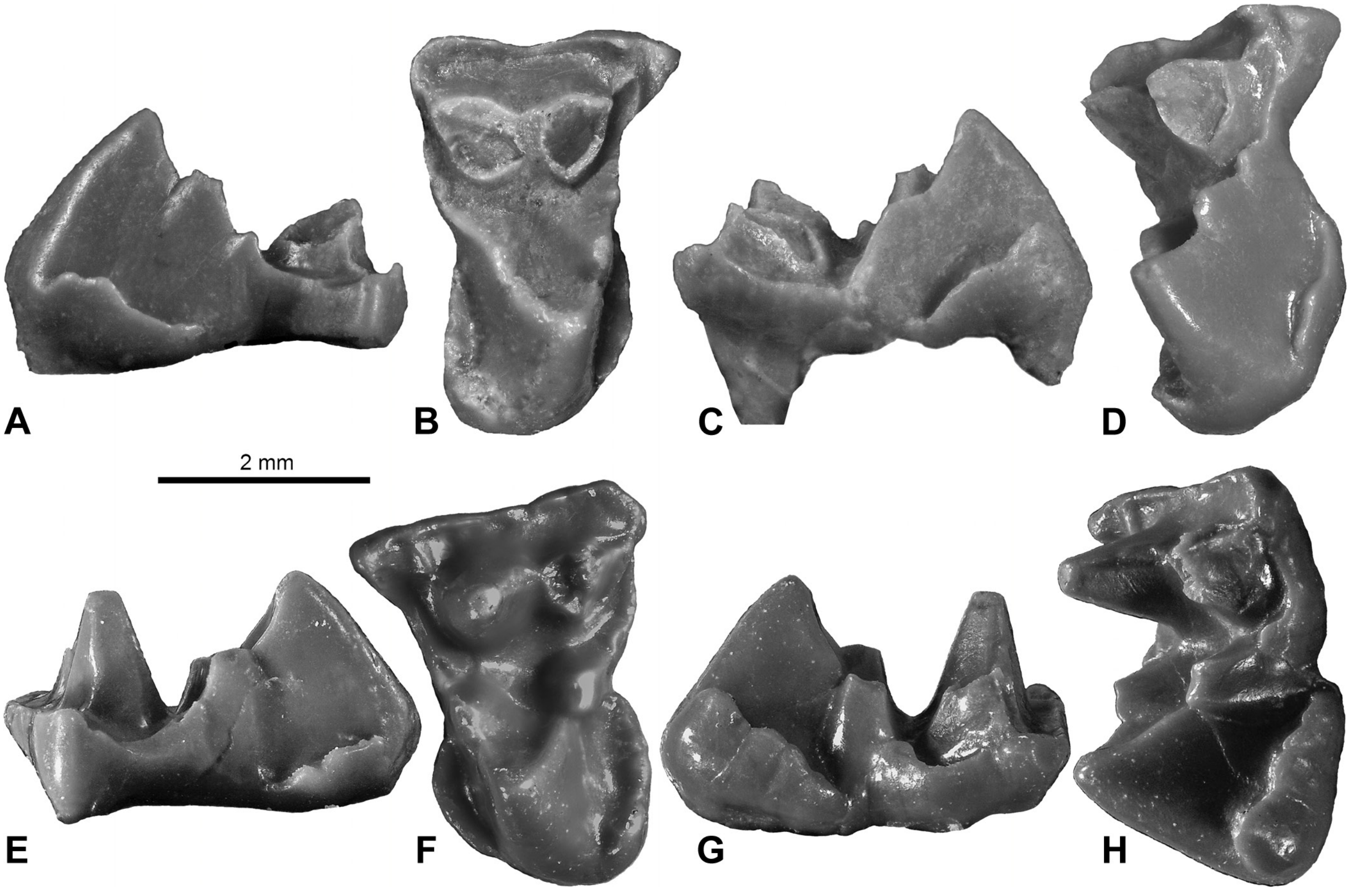

Figure 7A–H. Upper molars of *Prodiacodon crustulum*. LACM 32970, right M1-2. **A.** Mesial view. **B.** Occlusal view. **C.** Distal view. **D.** Oblique view of mesial side of crown showing doubled paraconule. UCMP 192146, left M1-2. **E.** Mesial view. **F.** Occlusal view. **G.** Distal view. **H.** Oblique view of distal side of crown showing doubled metaconule.

Alberta to Wyoming (Archibald 1982, Lofgren 1995, Cifelli et al. 2004, and Wilson 2014). Although a few latest Cretaceous mammals have been discovered in the San Juan Basin, New Mexico, the taxonomic diversity of its Lancian fauna is only beginning to be documented. Lack of a record of *Gypsonictops* here might well be a product of the small sample size. No occurrences of *Prodiacodon* or other leptictids have been reported in local faunas of indisputable Lancian age.

Puercan 1 records

In comparison to the Lancian, the number of local faunas referable to the Pu1 interval zone is much smaller. Geographically, well-sampled Pu1 local faunas are limited to Saskatchewan, Montana, Wyoming, and Colorado. Contemporaneous local faunas have yet to be discovered in the San Juan Basin, New Mexico, or farther to the south.

The local faunas in Saskatchewan come from two localities, Long Fall and Frenchman 1 (Fox 1997). Although Long Fall, particularly, is known from a large sample, neither local fauna has a record of leptictids. The ages of these local faunas are open to different interpretations. Both have records of typical Lancian NALMA mammals, including *Gypsonictops illuminatus* at Long Fall, but on the basis of the occurrence of the index taxon *Protungulatum* Sloan and Van Valen, 1965, they have been referred to the Pu1 interval zone by some workers. This poses the question, was the first occurrence datum of the appearance of *Protungulatum* in Saskatchewan precisely correlative with the Cretaceous/Paleogene boundary, which currently is defined by extinctions in the marine biota and the impact of an asteroid? Discussions of this question can be found in Cifelli et al. (2004, pp. 35–36) and Lofgren et al. (2004, pp. 64–65). Subsequently, description of the Spigot-Bottle local fauna in southeastern Montana posed a similar question (Archibald et al. 2011). The sample of mammals in this local fauna is dominated by fossils of typical Lancian species, including representatives of at least two species of *Gypsonictops*, but an isolated tooth indicates the presence of a species of *Protungulatum*.

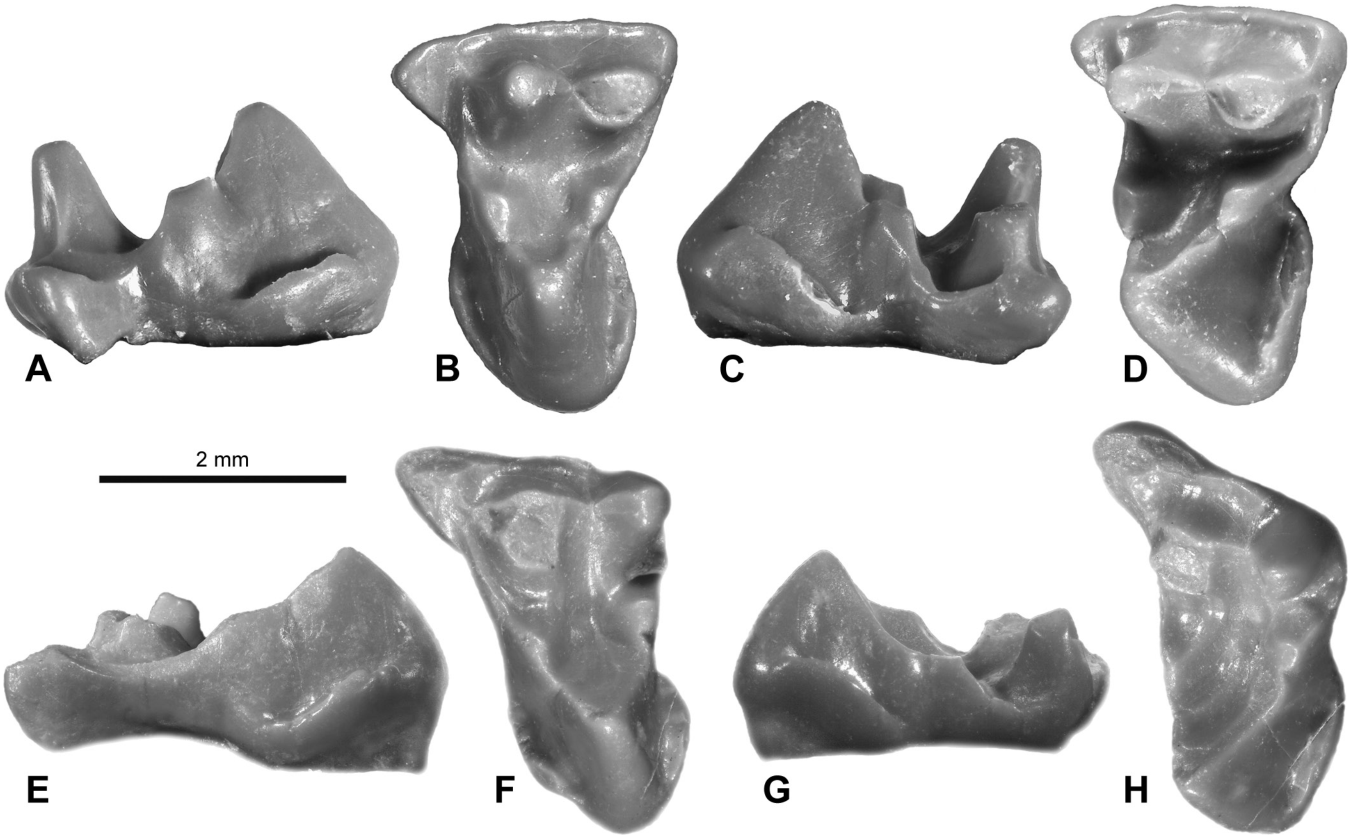

Figure 8A–H. Upper molars of *Prodiacodon crustulum*. UCMP 192145, left M1-2. **A.** Mesial view. **B.** Occlusal view. **C.** Distal view. **D.** Oblique view of mesial side of crown. UCMP 192147, left M3. **E.** Mesial view. **F.** Occlusal view. **G.** Distal view. **H.** Oblique view of distal side of crown.

Archibald (1982) did not report the presence of *Prodiacodon* or any other leptictidan in the Pu1 local faunas he analyzed; these are located primarily in Garfield County, Montana. Lofgren (1995) noted occurrences of *Gypsonictops* in several fossil assemblages in McCone County, Montana, of Pu1 age and interpreted them as time-averaged assemblages of Lancian and Puercan vertebrates. *Prodiacodon* was not represented in these or Pu1 local faunas lacking reworked nonavian-dinosaurian remains or other Lancian vertebrates.

In a review of samples of Pu1 local faunas in Garfield and McCone counties Wilson (2004) noted several isolated molars that, at that time, could not be assigned to known species. In a later study (Wilson 2014), two were tentatively referred to "*Prodiacodon* sp. A." In light of the analysis of a much larger sample of the dentition of *P. crustulum* reference of these teeth to *Prodiacodon* is suspect. More material is needed to verify a Pu1 occurrence of this genus or another leptictid in Montana.

Leptictids have not been reported as members of the Pu1 faunas found in the Mantua Lentil local fauna (Jepsen 1940) or the Ferris Formation, Wyoming (Eberle and Lillegraven 1998). The Littleton and South Bench localities in the Denver Basin, Colorado, also have yet to produce records of leptictids (Middleton and Dewar 2004).

Puercan 2 records

This interval zone is based on local faunas in the San Juan Basin, New Mexico. Some were discovered in the 19th Century and continue to be sources of new material. The most recent comprehensive review of the Paleocene stratigraphy of the San Juan Basin was prepared by Williamson (1996). He recognized several local faunas in the *Hemithlaeus kowalevskianus*/*Taeniolabis taoensis* zone, which is included within the Pu2 interval zone.

In the San Juan Basin the only Pu2 record of a leptictid comes from Williamson's (1996) locality 11, which includes the Black Toe locality of Standhardt (1980). The basis for Standhardt's record of a leptictid was seven isolated postcanines. These were compared to the dentition of *P. crustulum*, and she suggested they represented a new species of *Prodiacodon*. The postcanine dentition of this unpublished species was described as smaller than that of *P. crustulum*. Its upper molars have a single paraconule and the pre- and postcingula are not as elongated transversely as those of *P. crustulum*. The lower molars have relatively larger paraconids and lower trigonids than *P. crustulum*. She also specifically noted the absence of an entoconulid on m3. Williamson (1996, p. 35) tentatively accepted the allocation of this taxon to the Leptictidae but recognized it as "gen. et sp. nov. A".

Local faunas in Garfield and McCone counties, Montana, referable to the Pu2 interval zone have yet to be discovered and described. In southeastern Montana, localities in Makoshika State Park have yielded the Hiatt local fauna referable to either the latest Pu1 or earliest Pu2 interval zone (Hunter et al. 1997). This local fauna lacks a record of a leptictid. A smaller sample of a local fauna of similar age has been recovered at the PITA Flats locality, North Dakota (Hunter and Archibald 2002). It also lacks a record of a leptictid. Similarly, leptictids have yet to be found in the Pu2 interval zone of the Ferris Formation in Wyoming (Eberle and Lillegraven 1998).

To the north, *Prodiacodon* n. sp. (Rav W-1 local fauna) and *Prodiacodon* sp. (Croc Pot local fauna) have been reported from sites in Saskatchewan (Fox 1997), but the material on which they are based has yet to be described. Fox (1997, p. 78) noted, "The available specimens of *Prodiacodon* from Rav W-1 are isolated molars, but they show no closer resemblance to molars of *Gypsonictops illuminatus* than to those of other advanced species of *Gypsonictops*." He went on to argue that the ancestry of *Prodiacodon* and other Cenozoic leptictids did not include *G. illuminatus*.

Determination of the age of the Rav W-1 local fauna is a contentious issue (see Lofgren et al. 2004, p. 69). The local fauna contains mammals whose occurrences are usually taken as indicative of the Pu2 interval zone. To the south, Pu2 local faunas usually are preserved in strata deposited during the magnetostratigraphic chron C29n while the Rav W-1 local fauna is preserved in strata deposited in C29r. Fox and Scott (2011, pp. 546–547) suggested that the boundary between the Pu1 and Pu2 interval zones might well be time transgressive with Pu2 local faunas in the north being contemporaneous with Pu1 local faunas in other areas. Without implying a decision on this question, here the occurrence of *Prodiacodon* n. sp. is treated as being part of a Pu2 interval zone local fauna. The age of the Croc Pot local fauna, which has yet to be thoroughly analyzed, is considered to be "no older than Rav W-1" (Fox 1997, p. 77).

Puercan 3 records

Local faunas referable to this interval zone have been found in Montana, Wyoming, Utah, New Mexico, and possibly Texas (Lofgren et al. 2004). In earlier studies the age of the Garbani Channel and Purgatory Hill local faunas was given as Pu2/Pu3 undifferentiated (e.g., Clemens 2002 and references cited). The Pu3 interval zone is typified by local faunas in the Nacimiento Formation in the San Juan Basin, New Mexico. Initially its beginning was set at the first appearance of the multituberculate *Taeniolabis taoensis* Cope, 1882. Although the genus *Taeniolabis* Cope, 1882, is recognized in the Garbani Channel local fauna, *T. taoensis* has not been discovered. Recognizing the distinct possibility of complexity in the biogeographic and stratigraphic ranges of species of *Taeniolabis* within the Western Interior, the less precise reference to undifferentiated Pu2/Pu3 interval zones was adopted. This problem was discussed by Lofgren et al. (2004, pp. 68–69) who relaxed the first appearance criterion for the Pu3 interval zone to the first appearance of any species of *Taeniolabis*. Subsequent chronostratigraphic studies (Sprain et al. 2014) add support for an assignment of the Garbani Channel local fauna to the Pu3 interval zone, which is adopted here.

Lofgren et al. (2004, Table 2.2) record the presence of two genera of leptictids, *Prodiacodon* and *Palaeictops* in local faunas of the Pu3 interval zone. The origin of the record of "*Palaeictops* n. sp." appears to be an entry in a preliminary faunal list for the Purgatory Hill local fauna given by Van Valen and Sloan (1965, table 1). The record was based on five specimens, probably isolated teeth. Subsequently, in his provisional classification of the Leptictidae, Van Valen (1967, p. 232) noted the genus *Palaeictops* included an "(Undescribed species from Purgatory Hill); early Paleocene, North America." Just over a decade later Van Valen (1978, appendix 3, p. 69) published a list of all the placentals found at Purgatory Hill. He cited the presence of *Prodiacodon crustulum* and, cryptically, "about 5 other insectivorans." No mention was made of the presence of *Palaeictops*. Pending a comprehensive restudy of the Purgatory Hill local fauna it is appropriate to assume that currently *Prodiacodon*, probably *P. crustulum*, is the only leptictid documented in this local fauna.

To the south, neither a record of *Prodiacodon* nor another leptictid has been reported in the Pu3 local fauna from the Ferris Formation (Eberle and Lilligraven 1998) or the Wagonroad local fauna in Utah (Robison 1986). Leptictids have yet to be found at localities in the *Taeniolabis taoensis*/*Periptychus carinidens* zone in the San Juan Basin (Williamson 1996). They are absent in the small samples of possibly contemporaneous local faunas (Standhardt 1986) in the Big Bend area of Texas that are now thought to be of Torrejonian age (Leslie et al. 2014).

Torrejonian 1 records

The To1 interval zone includes localities formed during magnetostratigraphic chrons C28r, C28n, and C27r (**Lofgren et al. 2004**). The primary local faunas on which this interval zone was based are the Dragon local fauna, Utah, and material from several localities in the San Juan Basin (**Williamson 1996**). The latter are included in **Williamson's (1996)** *Periptychus carinidens/Protoselene ospisthacus* zone. The first appearance of *P. puercensis* is in local faunas in the San Juan Basin referable to this zone. *Prodiacodon* has yet to be discovered in the Dragon local fauna, but a leptictid, *Myrmecoboides* **Gidley, 1915**, n. sp., was reported by **Robison (1986)**. The local faunas in Utah and New Mexico are in strata deposited during C28n and C27r (**Lofgren et al. 2004**).

In northeastern Montana, the Farrand Channel and Horsethief Canyon localities have yielded large samples of microvertebrates (**Clemens and Wilson 2009**). *Prodiacodon* cf. *P. crustulum* has been found at the Farrand Channel locality. Both localities are in strata deposited during C28r (**Clemens and Wilson 2009**, **Sprain et al. 2014**) and are older than the To1 local faunas in Utah and New Mexico. Abundant representation of *Paromomys* **Gidley, 1923**, first appearing in To1 local faunas to the south, is the basis for reference of these two local faunas to the To1 interval zone.

Summary

The stratigraphically oldest records of members the Leptictida are four species of *Gypsonictops* that were members of many Judithian through Lancian NALMA local faunas. These occurrences come from a large number of localities in the Western Interior extending northward from the San Juan Basin into Alberta and Saskatchewan. Although a number of Asian Cretaceous genera have been included in the Gypsonictopidae, *Gypsonictops* is the only North American member of the family (**McKenna and Bell 1997**). The Torrejonian genus *Stilpnodon* Simpson, 1935, has been included in the family, but this reference has been regarded as doubtful (**McKenna and Bell 1997**). Currently, the Gypsonictopidae is usually interpreted as having become extinct at or slightly before the Cretaceous/Paleogene boundary (e.g., **Wilson 2014**).

In comparison to the Lancian NALMA, the Paleocene portion of the Pu1 interval zone is much shorter and known from fewer localities in an area extending from Colorado to Montana. In Montana it is at least 70 kyr but probably no more than ca. 200 kyr in duration (**Sprain et al. 2014**). If the Long Fall and Spigot-Bottle local faunas, which include records of *Gypsonictops* are regarded as referable to the Pu1 interval zone but of Cretaceous age, there is no evidence indicating that a leptictidan was present in the Western Interior at the beginning of the Paleocene.

A questionable record of a leptictid is known from a Pu2 local fauna in the San Juan Basin. In a preliminary analysis it was argued that it differs from *P. crustulum*, but, in the most recent analysis of this local fauna (**Williamson 1996**), it was tentatively listed as a leptictid "gen. et sp. nov. A." If the Rav W-1 and Croc Pot local faunas in Saskatchewan are referable to the Pu2 interval zone, the records of *Prodiacodon* sp. and *Prodiacodon* n. sp. in the faunal lists published by **Fox (1997)** provide documentation of the presence of leptictids in the Western Interior at this time. Geographically intermediate local faunas in southeastern Montana, North Dakota, and Wyoming lack records of leptictids.

The oldest well-substantiated records of *Prodiacodon* are Pu3 interval zone occurrences of *P. crustulum* from the Garbani Channel localities and, probably, the Purgatory Hill local fauna in northeastern Montana. Leptictids have yet to be found in the other known Pu3 local faunas in Wyoming, Utah, and New Mexico.

The documented diversity of leptictids in the To1 interval zone increases first with records of *Prodiacodon* cf. *P. crustulum* in northeastern Montana and younger To1 records of *Myrmecoboides* n. sp. in the Dragon local fauna, Utah, and *P. puercensis* in the San Juan Basin, New Mexico. The post-To1 history of leptictids in North America has been summarized by **Gunnell et al. (2008)**.

DISCUSSION

Reconstruction of the dentition of *Prodiacodon crustulum*

Since 1977 the hypodigm of *P. crustulum* has been greatly increased. It now includes over 100 complete and fragmentary isolated teeth. The only postcanines found in association are p2, a fragment of p4, and p5 preserved in a fragment of dentary. Identifications of these and other elements of the postcanine dentition are based primarily on comparisons with *P. puercensis* and dentitions of more recent leptictids. This reconstruction also is based on the assumption that only one species of leptictid, *P. crustulum*, was a member of the Garbani Channel fauna.

In reconstructing the dentition of *Prodiacodon crustulum* from isolated teeth **Novacek (1977)** made comparisons with the dentition of the Torrejonian leptictid *P. puercensis* and more derived species of the genus. Then, as now, the published sample of the upper and lower dentitions of *P. puercensis* consisted of elements of the type

(AMNH 16011, a P5) and paratype (AMNH 16748, full upper and lower postcanine dentitions). T.E. Williamson (pers. com. 2014) reviewed the unpublished material of *P. puercensis* in the collections of the New Mexico Museum of Natural History and Science. He found that in comparison to the dentition of the paratype these teeth were of simpler morphology lacking many of the small, accessory conules and conulids. The ranges of intraspecific variation in the dental morphology of *P. puercensis* remain to be adequately determined.

If correctly identified, the enlarged sample of isolated teeth requires some modification of Novacek's characterization of the dentition of *P. crustulum*. As he noted, in comparison with the published dimensions of the teeth preserved in the type and paratype of *P. puercensis* (Novacek 1977, Tab. 2), most of the postcanines of *P. crustulum* are smaller (Tab. 2). One possible exception is M3. Upper molars of *P. crustulum* were characterized as having a "doubled" paraconule. Of the 15 M1-2s that preserve this area on six the paraconule is doubled or weakly subdivided; the other nine have a single paraconule. Lower molars of *P. crustulum* were described as lacking an entoconulid on m1-2 but this cusp was present on m3. The enlarged sample shows that the presence of an entoconulid on the lower molars is variable. One or more entoconulids are developed on the talonids of 14 of the 38 of the m1-2s of *P. crustulum* on which this area is preserved. An entoconulid is present on the talonids of three of the six m3s in the sample. The blunt mesial ends of the teeth identified as p5s of *P. crustulum* differ from the salient mesial ends of p5s in the other species of *Prodiacodon*. Identification of these teeth as permanent premolars hinges on the root structure of the distal premolar preserved in the fragment of dentary (Fig. 2) and needs to be tested through the discovery of dentaries preserving the distal premolar and one or more molars.

Phylogenetic relationships of *Prodiacodon crustulum*

Novacek (1977, p. 36) argued that *Prodiacodon crustulum* was the most primitive species of the genus and cited presence of a "doubled paraconule" as possibly a defining apomorphy of the genus. The isolated molars in the new hypodigm of *P. crustulum*, if correctly identified, document variation between a single and a doubled morphology of cusps in the paraconule region. Variation in presence or absence of miniscule stylocones, a lesser degree of development of cusps on pre- and postcingula, and variation in presence of mesoconids and entoconids on the lower molars support the hypothesis that they are precursors of the more derived dental morphology of *P. puercensis*. Overall, the new data support Novacek's (1977) conclusion that *P. crustulum* is the most primitive known species of *Prodiacodon*.

The study of the interrelationships of Paleocene and Eocene leptictids (*Myrmecoboides, Prodiacodon, and Palaeictops*) carried out by Novacek (1977) involved one postcranial and 16 dental characters and was carried out manually. Although noting earlier studies dealing with the broader relationships of leptictids (e.g., Butler 1972, McKenna 1975), he focused his analysis on the phylogenetic interrelationships of these three early leptictids. Almost a decade later, Gunnell et al. (2008, see fig. 6.2) reevaluated the content of the Leptictidae. They accepted Novacek's (1977) tentative interpretation that *Myrmecoboides* possibly split off prior to the differentiation of *Prodiacodon* and *Palaeictops*. If correct, the last common ancestor of *Myrmecoboides*, first recorded in the To1 interval zone, and *Prodiacodon* would have to have been in the Pu1 interval zone if not earlier. Gunnell et al. (2008) added the poorly known Paleocene genera *Xenacodon* Matthew and Granger, 1921, only known from a Tiffanian 4 (Ti4) local fauna, and, possibly, *Leptonysson* Van Valen, 1967, only known from a To3 local fauna, as basal members of the Leptictidae. As with *Myrmecoboides*, inclusion of these two genera implies long ghost lineages and differentiation in the Pu1 interval zone if not earlier.

Gunnell et al. (2008) also reviewed different interpretations of the broader phylogenetic relationships of the Leptictidae. They followed Novacek (1986) in recognizing a clade, the Leptictida, including the families Leptictidae and Gypsonictopidae. Kielan-Jaworowska et al. (2004) had limited the content of the latter family to the North American Late Cretaceous species of *Gypsonictops*. The hypothesis of close phylogenetic relationship of these two lineages had its origin when Simpson (1927) established the genus *Gypsonictops*, based on isolated upper molars. He emphasized the importance of *Gypsonictops* in providing the first strong indication of the presence of eutherians in North American latest Cretaceous mammalian faunas, which were dominated by multituberculates and marsupials. Also, recognizing the morphological similarity of their upper molars, Simpson (1927, p. 7) noted the "very probable leptictid affinities" of *Gypsonictops*.

With newly discovered material from the Lance Formation, in 1951 Simpson again turned his attention to an analysis of *Gypsonictops*. Based on isolated teeth he (Simpson 1951, legend of fig. 3) tentatively proposed a "hypothetical reconstruction of P^4-M^3 of a Cretaceous insectivore, cf. *Gypsonictops*." He also revised his interpretation of the phylogenetic relationships of *Euangelistes petersoni* Simpson, 1929. Its holotype is a fragment of a dentary that preserves the two distal-most premolars and three molars. He originally thought *E. petersoni* was a marsupial, but then recognized that it was a eutherian. Suggesting that his hypothetical reconstructions of the dentitions of cf. *Gypsonictops* and *Euangelistes* **Simpson, 1929**, might represent a single taxon (see **Simpson 1951**, fig. 7), he explored the possibilities of phylogenetic relationships of *Gypsonictops* with various North American and Asian mammals. Although not fully retracting his support, he was more circumspect in allying *Gypsonictops* with members of the Leptictidae.

Lillegraven (1969) described a large sample of *Gypsonictops* from the Scollard Formation in Alberta. Making extensive comparisons with the well-known Tertiary genus *Leptictis*, he argued that *Gypsonictops* could be in the direct ancestry of most Cenozoic leptictids and classified it in a separate subfamily within the Leptictidae. Morphological similarities of their upper and lower molars support the hypothesis of close phylogenetic relationship. In contrast, differences in the morphology of their premolars still argue against a strict ancestor-descendant relationship.

McKenna (1975) recognized the probability of close phylogenetic relationship between the Leptictidae, *Gypsonictops*, and several other groups of eutherians and included them in the clade Leptictida. Subsequently, **Novacek (1986)** revised McKenna's concept of the Leptictida limiting its content to *Gypsonictops*, tentatively classified in a separate family, the Gypsonictopidae, and the Leptictidae. **Gunnell et al. (2008)** reviewed the different interpretations of the content and phylogenetic relationships of the Leptictida. They followed **Novacek (1986)** in limiting the clade to include the families Leptictidae and Gypsonictopidae as well as accepting **Kielan-Jaworowska et al.'s (2004)** restriction of the content of the latter family to the North American Late Cretaceous species of *Gypsonictops*. The ancestry of the Leptictida remains unknown. The fossil record suggests that the Leptictidae had its origin outside of the currently sampled areas of the North American Western Interior, and during the early Puercan *Prodiacodon* immigrated into this area (**Clemens 2010**, **Wilson 2014**).

Several more recent studies of the phylogenetic interrelationships of eutherian mammals considered the relationship of *Gypsonictops* and the Leptictidae. For example, in their analyses **Wible et al. (2007**, **2009**) included *Gypsonictops* and the derived leptictid *Leptictis*. This study indicated that these two genera were sister taxa, which supported **Novacek's (1986**) interpretation of the nature and content of the Leptictida. Contrary to some earlier studies, the Leptictida was ranked as a eutherian group outside the mammalian crown group Placentalia **Owen, 1837**. They also considered the content and phylogenetic relationships of the Afrotheria a group first recognized in molecular studies. Here they included representatives of the core afrotherians—proboscideans, hyracoids, orycteropodids, and macroscelids—and found that the Afrotheria nested within the Placentalia rather than taking a basal position as suggested in other studies.

Other approximately contemporaneous or more recent studies explored the possible phylogenetic relationships between the afrotherian macroscelids and, particularly, louisinine and apheliscine "hyposodontids" (review in **Hooker and Russell 2012**). *Leptictis* was frequently included in these analyses. **Hooker and Russell (2012)** went farther and included both *Gypsonictops* and *Prodiacodon*. Their analysis supported the Leptictida (*sensu* **Novacek 1986**) as a monophyletic group. Increasing their ranks to family level, the louisinids and alpheliscids were tentatively considered to be among the stem members of the Macroscelidea **Butler, 1956**, and the Leptictida its sister group.

Subsequently, **O'Leary et al. (2013)** addressed questions of the phylogenetic pattern and tempo of the origins and early diversification of placental mammals. In their dataset the Leptictidae was represented by *Leptictis*. *Prodiacodon crustulum* was not included in their dataset but cited as establishing the oldest record of the family. Their analysis supported the hypotheses that leptictids were members of the Afrotheria and that this group did not originate in Africa. A limitation of their study is that *Gypsonictops* as well as a large number of Cretaceous and early Paleocene taxa represented primarily by dental material were excluded (**O'Leary et al. 2013**, supplementary materials, p. 9). Although knowledge of their skeletal morphologies is limited, their inclusion would have provided critical data elucidating mammalian evolution during this period of Earth history.

CONCLUSIONS

As part of an ongoing analysis of the composition of the Garbani Channel local fauna, the primary goal of this study is to revise the description of the dentition of *Prodiacodon crustulum* on the basis of a larger hypodigm than was available to **Novacek (1977)**. With the exception of one fragment of a dentary containing p2, a fragment of p4, and p5, the new collection includes only isolated teeth. Using the type and paratype of *P. puercensis* as models, the dentition of *P. crustulum* was reconstructed revealing some characters that add support to **Novacek's (1977)** diagnosis of the species and his analysis of its phylogenetic relationships to other species of this genus.

Many but not all recent phylogenetic analyses support the monophyly of the Leptictida. Dental differences, particularly those of the premolars, argue against a direct ancestor-descendant relationship of *Gypsonictops* and *Prodiacodon* as well as later leptictids. Absence of leptictids in Lancian local faunas of the North American Western Interior supports the hypothesis that they were immigrants into this area after the Cretaceous/Paleogene boundary probably arriving during Pu2 if not before.

Recent studies support the interpretation of a sister group relationship between the Leptictida and macrosceledid afrotherians. The Puercan through Torrejonian range of *Prodiacodon* in North America suggests the area of origin of afrotherians might not have been Africa. If the clade Leptictida is monophyletic, the differentiation of the macrosceledid lineage would have occurred prior to the Cretaceous/Paleogene boundary.

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