Eoconodon ("Triisodontidae," Mammalia) from the Early Paleocene (Puercan) of northeastern Montana, USA

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ABSTRACT

The uppermost Hell Creek and Tullock Formations of Garfield and McCone Counties, northeastern Montana, have yielded large samples of earliest Paleocene (Puercan North American Land Mammal 'Age') local faunas. These are allocated to either the earliest Puercan (Pu1) interval zone or an undifferentiated Pu2/Pu3 interval zone of middle and/or late Puercan age. *Eoconodon* ("Triisodontidae") is absent from Pu1 local faunas of northeastern Montana, but is represented by two species (*E. nidhoggi* and *E. hutchisoni*, new species) in Pu2/Pu3 interval zone local faunas. Morphology of their cheek teeth, presence of Hunter-Schreger bands in their enamel, and relatively large mandibular horizontal ramus and symphysis (known only for *E. hutchisoni,* new species) are similar to those of mesonychians. These derived characters suggest that the species of *Eoconodon* included early eutherian experiments in evolution of large body size and a predatory mode of life.

Species of *Eoconodon* or a closely related sister group are not known from latest Cretaceous local faunas of the Western Interior. The oldest records of the genus are limited to the Pu1 Mantua Lentil local fauna in the Big Horn Basin and UW locality 91015 in the Ferris Formation, Wyoming. They provide support for the hypothesis that *Eoconodon* was an immigrant entering the Western Interior during the Pu1 interval zone. Samples of Pu2 and Pu3 local faunas document differentiation of the genus into three species known primarily from the San Juan Basin, New Mexico, and two other species currently known in local faunas of Montana and other northern localities.

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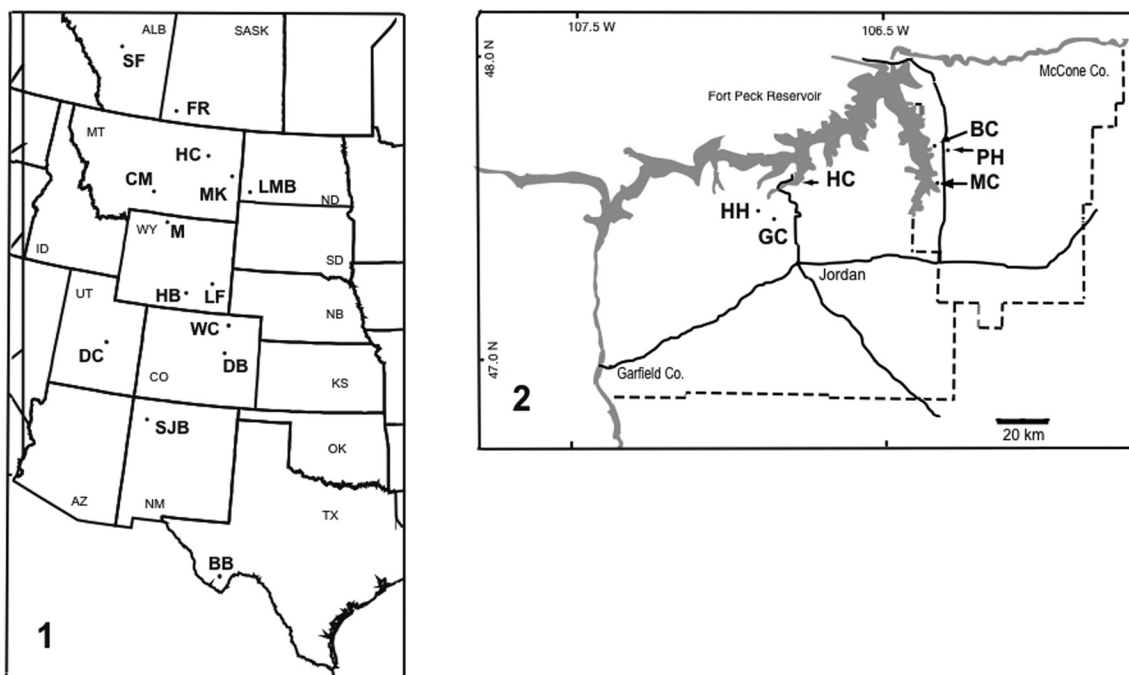
FIGURE 1. Locality maps. Figure 1.1: North American Western Interior. More comprehensive maps of localities are presented by Cifelli et al. (2004, Figure 2.2) for the Lancian and Lofgren et al. (2004, Figure 3.1) for the Puercan. Figure 1.2: Localities in Garfield and McCone Counties, Montana. Abbreviations of locality names in Figure 1.1: **BB**—Big Bend area, Tornillo Formation; **CM**—Crazy Mountain Basin, Bear Formation (Pu2/Pu3); **DB**—Denver Basin, Denver Formation (Pu1, Pu2); **DC**—Dragon Canyon, North Horn Formation (Lancian, Pu2, Pu3); **FR**—Frenchman and Ravenscrag Formations (Lancian, Pu1); **HB**—Hanna Basin, Ferris Formation (Lancian, Pu1, Pu2, Pu3); **HC**—Sites in Garfield and McCone Counties, Hell Creek and Tullock Formations (Lancian, Pu1, Pu2/Pu3), see Figure 1.2 for a detailed map of the area; **LBM**—Little Missouri Badlands, Hell Creek Formation (Lancian); **LF**—Powder River Basin, Lance Formation (Lancian); **M**—Mantua Lentil, Polecat Bench Formation, Big Horn Basin (Pu1); **MK**—Makoshika State Park, Fort Union Formation, (Pu2); **SF**—Scollard Formation, Alberta (Lancian); **SHB**—San Juan Basin, Kirtland and Nacimiento Formations (Lancian, Pu2, Pu3); **WC**—Weld County, Laramie Formation(Lancian)

Abbreviations in Figure 1.2: **BC**—Localities in the valley of Bug Creek; **GC**—Garbani Channel localities; **HC**—Valley of Hell Creek: **HH**—Hell's Hollow localities; **MC**—McGuire Creek localities; **PH**—Purgatory Hill.

INTRODUCTION

Fossil localities in the Garbani Channel deposits and other units of the Tullock Formation, Garfield and McCone Counties, northeastern Montana, have yielded large samples of latest Cretaceous (Lancian) and early Paleocene (Puercan and Torrejonian) vertebrates (Clemens 2002). Archibald (1982), Lofgren (1995), and Wilson (2004, 2005) have analyzed the Lancian and earliest Puercan (Pu1 interval zone) mammalian faunas of the area. Torrejonian local faunas have been analyzed by Clemens and Wilson (2009). In contrast samples of Pu2/Pu3 (undifferentiated)

Puercan local faunas have yet to receive comparable attention. The primary goal of this paper is to help fill this gap through description and analysis of new material from the Pu2/Pu3 deposits in the Tullock Formation representing two species of *Eoconodon* ("Triisodontidae," Mammalia).

Comparisons are made with species of *Eoconodon* from other areas of the Western Interior, particularly the San Juan Basin, New Mexico (Williamson 1996, Clemens and Williamson 2005). The paleobiogeographic distribution of currently documented occurrences of these species provides support for the hypotheses that immigration played a significant role in the evolution of Puercan

faunas after the extinctions marking the Cretaceous-Tertiary boundary and Puercan mammalian faunas of the Western Interior were characterized by distinct paleobiogeographic provincialism.

GEOLOGICAL AND STRATIGRAPHIC SETTINGS

Most of the new material described here was derived from the Garbani Channel deposits, part of the Tullock Formation, exposed in Garfield County, Montana (Archibald 1982, Clemens 2002, Figure 1). A smaller sample described by Van Valen (1978) was derived from another channel deposit in the Tullock Formation exposed at the top of Purgatory Hill, McCone County, Montana. These localities are considered to be approximately contemporaneous and Puercan in age (Clemens 2002, Lofgren et al. 2004).

The Puercan NALMA has been subdivided into three units designated Pu1 through Pu3. Pu2 and Pu3 were initially typified by occurrences of mammals in the San Juan Basin, New Mexico (see Lofgren et al. 2004). Probably because of biogeographic provincialism many of these taxa are not known in local faunas of the northern Western Interior (Montana, North Dakota, Alberta, and Saskatchewan) thus preventing direct biochronological correlations. To reflect this uncertainty the local faunas of the Garbani Channel and approximately contemporaneous sites in the northern Western Interior are designated Pu2/Pu3 undifferentiated (see Clemens 2002, Clemens and Williamson 2005).

PALEONTOLOGICAL METHODS

All cited fossil localities in Garfield and western McCone counties are cataloged in the records of the University of California Museum of Paleontology (UCMP) and their identifying numbers presented in the following format: V-73080. Catalog numbers of individual specimens are preceded by their museum acronyms (see abbreviations). Online locality and specimen catalogs are available at http://ucmpdb.berkeley.edu/ Measurements of specimens were obtained with dial calipers and recorded to the nearest tenth of a millimeter. Ages cited in the text are taken from Wilson (2004, 2005) who recalculated the values for tephra presented in Swisher et al. (1993) and magnetostratigraphic chron boundaries published by Berggren et al. (1995). Following Renne et al. (1998) and Knight et al. (2003 erratum), the value of 65.58 ± 0.04 m.y. was adopted for the Cretaceous/Tertiary boundary,

and their conversion formula was used to recalculate the other age determinations.

Institutional Abbreviations

AMNH – American Museum of Natural History, New York, New York; LSUMG – Louisiana State University, Museum of Geosciences, Baton Rouge, Louisiana; LACM – The Natural History Museum of Los Angeles, California; NMMNH – New Mexico Museum of Natural History and Science, Albuquerque, New Mexico: PU – Princeton University, specimens now in the collections of the Yale Peabody Museum, New Haven, Connecticut; UCMP – University of California Museum of Paleontology, Berkeley, California; UMVP – The Museum of Paleontology, University of Minnesota, Minneapolis, Minnesota; UW – Collection of fossil vertebrates, departmental scientific collections, Department of Geology and Geophysics, The University of Wyoming, Laramie, Wyoming.

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linneaus, 1758
Cohort PLACENTALIA Owen, 1837
Family "TRIISODONTIDAE" Trouessart, 1904
Eoconodon Matthew and Granger, 1921

Comments. Recent analyses of the suprafamilial relationships of the "Triisodontidae" within the Placentalia have been inconclusive. The family is left *incertae sedis* within the cohort. Following Van Valen (1978) *Eoconodon coryphaeus* is recognized as the type species of the genus. Biogeographically, the species of *Eoconodon* fall into two groups, those known only from the San Juan Basin and possibly Texas, and those known only from localities in Wyoming, Montana, and Saskatchewan. To facilitate this study the type and other species from the San Juan Basin (*E. gaudrianus* and *E. ginibitohia*) as well as possible occurrences in Texas are briefly reviewed. Then records of *Eoconodon* from localities in the northern Western Interior, including descriptions and analyses of new material from Montana, are presented.

Species known from the southern Western Interior, New Mexico, and possibly Texas

Eoconodon coryphaeus (Cope, 1885)

Comments. *Eoconodon coryphaeus,* the largest known species of genus, is represented by large samples from the *Hemithlaeus kowalevskianus - Taeniolabis taoensis* Zone (Pu2) and smaller samples from the *Taeniolabis taoensis - Periptychus carinidens* Zone (Pu3) of the San Juan Basin (Wil-

TABLE 1. Dimensions of the cheek teeth of species of *Eoconodon.*

			Length			Width	
		N	OR	M	N	OR	M
P4	*E. coryphaeus*	7	8.60-11.00	9.70	9	10.00-11.90	10.93
	E. hutchisoni	4	7.70-8.70	8.49	3	8.50-9.90	9.20
	E. gaudrianus	1	6.40				
	E. nidhoggi	1	6.90		1	6.70	
M1	*E. coryphaeus*	17	9.80-11.30	10.52	16	11.10-14.10	12.88
	E. hutchisoni	3	8.30-9.20	8.62	1	11.05	
	E. gaudrianus	2	8.50-8.70	8.60	1	11.90	
M1-M2	*E. nidhoggi*	2	6.70-6.90	6.80	3	8.50-8.70	8.57
M2	*E. coryphaeus*	15	9.30-13.50	11.22	16	11.40-16.90	15.34
	E. hutchisoni	5	8.65-9.15	8.89	7	11.00-12.45	11.99
	E. gaudrianus	1	8.70				
M3	*E. coryphaeus*	12	7.20-12.30	8.66	13	11.60-14.50	13.71
	E. hutchisoni	3	5.50-6.20	5.90	3	8.75-9.35	9.13
p4	*E. coryphaeus*	16	10.70-13.90	12.40	16	5.90-7.80	6.70
	E. hutchisoni	4	8.80-9.60	9.20	6	4.90-6.50	5.40
	E. gaudrianus	2	9.00-11.00	10.00	2	5.00-6.20	5.60
	E. ginibitohia	1	6.80		1	3.40	

			Length			Width Trigonid			Width Talonid	
		N	OR	M	N	OR	M	N	OR	M
m1	*E. coryphaeus*	18	10.20-12.20	11,0	16	6.80-8.30	7.50	18	7.20-9.20	8.20
	E. hutchisoni	6	5.60-9.90	9.28	6	5.55-6.45	6.00	6	5.65-6.70	6.18
	E. gaudrianus	1	8.60							
	E. nidhoggi	2	7.60-7.70	7.65	3	4.30-5.50	4.80	1	4.30	
	E. copianus	1	9.40		1	5.30		1	4.50	
m2	*E. coryphaeus*	21	11.40-13.70	12.30	25	7.00-11.20	9.20	19	7.20-11.00	8.90
	E. hutchisoni	4	9.30-10.10	9.60	7	6.40-7.50	6.80	6	5.80-6.50	6.20
	E. gaudrianus	2	8.90-9.40	9.15	2	6.30-7.40	6.85	1	7.10	
	E. nidhoggi	4	6.80-7.55	7.21	4	4.60-4.80	4.73	4	4.40-4.60	4.50
	E. ginibitohia	1	7.00		1	4.60		1	4.20	
m3	*E. coryphaeus*	16	11.50-14.40	13.20	16	7.00-10.30	8.60	14	6.30-9.00	7.40
	E. hutchisoni	5	8.00-8.75	8.30	4	5.30-6.20	5.70	4	4.60-5.00	4.80
	E. gaudrianus	2	8.80-9.50	9.10	1	6.50		1	5.60	
	E. nidhoggi	4	7.40-7.60	7.53	4	4.40-5.60	4.41	4	3.70-4.70	4.33
	E. ginibitohia	1	6.90		1	4.30		1	3.30	

liamson 1996). The species has yet to be certainly identified from localities outside the San Juan Basin.

The nomenclatorial history of *Eoconodon coryphaeus* is long and complex (see Matthew 1937, Van Valen 1978, Williamson 1996), but an adequate revised diagnosis of the species has yet to be developed. Remedying this situation will require a thorough analysis of the large samples now available from the San Juan Basin, a task beyond the scope of this paper. Currently the primary if not sole character usually cited to distinguish *E. coryphaeus* from the other species of *Eoconodon* is the larger size of its postcanine dentition (Table 1). For the purposes of this study, the difference in dental dimensions is deemed sufficient as a provisional diagnosis.

Eoconodon gaudrianus (Cope, 1888)

Diagnosis. Williamson (1996, p. 41) essentially followed Matthew (1937) and summarized the diagnosis of the species as follows: "This species differs from *Eoconodon coryphaeus* in its smaller size. It differs from *Goniacodon* in the greater transverse diameters of the molars and the unreduced M_3."

Comments. The mean values of the lengths of m2 and m3 (Table 1) suggest that m2 of *Eoconodon gaudrianus* was slightly longer than m3, but the samples are small and probably do not adequately reflect individual variation in size of the dentition. AMNH 3200, the type specimen, includes fragments of a skull, dentaries, and a calcaneum. Reasonably well preserved P4 and M3 are present in the fragment of maxillary; one dentary includes remains of m2 and m3. Stressing that little beyond the margins of the alveoli of these lower molars are preserved, the crown length of m2 (alveolar length ca. 9.0 mm) might have been greater than that of m3 (alveolar length ca. 8.8 mm), however, an allowance for a posteriorly projecting hypoconulid region of m3 must be made.

Matthew (1937) and later workers appear to have placed greater weight on the morphology of the somewhat better preserved lower molars of AMNH 4029 and AMNH 58116. On the basis of this material it appears that *Eoconodon gaudrianus* is characterized by presence of an m3 with a length equal to or longer than that of m2.

A survey of the dentitions of *Protungulatum* as well as *Baioconodon* and *Oxyclaenus*, which have been considered to be closely related archaic ungulate sister groups (e.g., Archibald 1998), suggests the working hypothesis that an m3 of approx-

imately equal or greater length than m2 was the primitive condition for *Eoconodon.*

Occurrences. In contrast to *Eoconodon coryphaeus*, *E. gaudrianus* is a rare species in *Hemithlaeus kowalevskianus - Taeniolabis taoensis* Zone (Pu2) local faunas of the San Juan Basin and unknown in the smaller samples of *Taeniolabis taoensis - Periptychus carinidens* Zone (Pu3) local faunas (Williamson 1996). The localities at which the type and other specimens from the E.D. Cope collection referred to *E. gaudrianus* by Matthew (1937) are not precisely recorded. Williamson (1996) noted occurrences of *E. gaudrianus* in three local faunas in the *Hemithlaeus kowalevskianus – Taeniolabis taoensis* Zone (Pu2).

Eoconodon ginibitohia Clemens and Williamson, 2005

Revised Diagnosis. Size: dimensions of p4 and m2-3 either just fall within or are slightly smaller than the observed ranges of variation of homologous teeth, where known, of *Eoconodon nidhoggi* and are distinctly smaller than the observed ranges of variation of dimensions of *E. gaudrianus, E. coryphaeus,* the new species of *Eoconodon* described below, and probably *E. copanus.* The m2-3 are distinguishable from those of *E. nidhoggi* by: 1) greater reduction of the paraconid; 2) talonid cusps of m2 and, probably, m3 are relatively smaller and less distinct; 3) the basal cingulid is not as well developed and incomplete across the labial side of the trigonid, and 4) the talonid of m3 is narrower. In the single available specimen, length of m3 is very slightly less than that of m2, and the trigonid and particularly the talonid of m3 are narrower than those of m2 (Table 1).

Comments. The presence of a new species of *Eoconodon* in the *Hemithlaeus kowalevskianus – Taeniolabis taoensis* Zone (Pu2) of the San Juan Basin, was first recognized by Williamson (1996) on the basis of a single, fragmentary mandible. (NMMNH P21622) preserving p4 and m 2-3 that was described and named *E. ginibitohia* by Clemens and Williamson (2005). The taxon referred to as *E.* cf. *E. gaudrianus* in the original diagnosis of *E. ginibitohia* is the new species of *Eoconodon* described below.

?*Eoconodon* sp.

Standhardt (1986) described several fragmentary teeth and postcranial bones from LSUMG locality VL-107 ("Glen Eleven"), upper Javelina Member, Tornillo Formation and referred these to *Eoconodon coryphaeus*. Williamson (1996, p. 66) argued that these specimens, possibly from the

same individual, are too fragmentary to allow a generic determination but suggest the presence of a large "triisodontid." Standhardt (1986, 1995) also noted the possible presence of *Eoconodon* in LSUMG locality VL-108, which she thought was of late Puercan age primarily on the basis of paleo-magnetic evidence. On the basis of faunal composition Williamson (1996, p. 66-67) suggested a Torrejonian correlation. Additional material is needed to validate this purported occurrence.

Species known from the northern Western Interior, Wyoming, Montana, and Saskatchewan

Eoconodon nidhoggi Van Valen, 1978

Holotype. UMVP 1471, left m3 (Van Valen 1978, Plate 4, Fig. 6).

Type Locality. Purgatory Hill (UCMP loc. V-71202), Tullock Formation, McCone County, Montana, Pu2/Pu3 (Van Valen and Sloan 1965).

Referred Postcanines and Localities. In establishing this species Van Valen (1978) did not refer any other specimens from Purgatory Hill or other localities in McCone or Garfield Counties. Casts of several isolated teeth from Purgatory Hill in the UMVP collection identified as *Eoconodon* sp. have been distributed to several museums. One of these, a cast of an isolated P4 (UMVP 1475), might represent a tooth referable to *E. nidhoggi*. The majority of the specimens currently included in the hypodigm of the species are from localities in Garfield County, Montana.

M1 or **M2**, UCMP 156122 (V-72201), UCMP 170847, 189400 (V-73080), UCMP 156110 (V-75230); **m1**, LACM 32925 (V-72125), UCMP 145325 (V-73080), UCMP 192015 (V-73082); **m2**, UCMP 192014 (V-72129), UCMP 145328, 170848, 185983, 186602 (V-73080); **m3**, UCMP 145323 (V-72126), UCMP 145330, 186414 (V-73080).

Revised diagnosis. As far as they are known the lengths and widths of the molars are smaller than of those of the other species of *Eoconodon* except *E. ginibitohia*. Dimensions of m2 and m3 of the type and only specimen of *E. ginibitohia* are either slightly smaller than or fall within the lower end of the observed ranges of variation in the small samples of homologous teeth of *E. nidhoggi* (Table 1). The m2 and m3 of *E. nidhoggi* are distinguishable from those of *E. ginibitohia* by: 1) relatively larger paraconids; 2) talonid cusps of m2 and, probably, m3 are relatively larger and more distinct; 3) the basal cingulid is better developed and complete across the labial side of the trigonid, and 4) the talonid of m3 is broader than its trigonid. *E. nidhoggi*

resembles *E. coryphaeus* in the greater length of m3 relative to m2. In *E. ginibitohia* the length of m3 is slightly smaller (99%) than that of m2. In contrast, the mean length of m3 of the new species described below is distinctly shorter (77%) than that of m2.

Occurrences. In addition to Purgatory Hill, the type locality (V-71202) in McCone County, specimens of *Eoconodon nidhoggi* have been found the following localities of Pu2/Pu3 age in the Tullock Formation, Garfield County: V-72125, V-72126, V-72129, V-72201, V-73080, V-73082, and V-75230. Specimens tentatively referred to *E. nidhoggi* have been reported from the following localities outside Garfield and McCone counties: Buckley (1994) identified isolated upper and lower molars from Simpson Quarry, Bear Formation, south central Montana, as *Eoconodon* sp. cf. *E. nidhoggi*. The age of this local fauna cannot be refined beyond Pu2/Pu3 undifferentiated (Buckley 1994; Lofgren et al. 2004). Noting its diminutive size Hunter et al. (1997) described a small fragmentary lower molar from the Hiatt South Locality, Fort Union Formation, southeastern Montana and tentatively referred it to *E. nidhoggi*. On biostratigraphic grounds Hunter et al. (1997) argued for a Pu2, possibly early Pu2, age assignment for this locality (Lofgren et al. 2004). Finally Johnston and Fox (1984) identified three fragmentary teeth found at Rav W-1, Saskatchewan, as ?*Eoconodon nidhoggi*. Considering the stage of evolution of some of its members Fox (1997) tentatively assigned a Pu2 age to this local fauna, but Lofgren et al. (2004) tentatively assigned it to the Pu3 interval zone on the basis of the presence of a species of *Taeniolabis*.

Description and comparisons. Tentative identifications of the P3 and P4 of the two species of *Eoconodon* currently recognized in the Pu2/Pu3 of northeastern Montana are based on comparisons with the dentition of *E. coryphaeus* from the San Juan Basin. In the latter species the crowns of P3 and larger P4 are dominated by a large, bulbous paracone, which can be slightly canted posteriorly. On both premolars, a low protocone, relatively larger on P4, is present (see Matthew 1901, figure 12). The width of the crown of P4 is approximately the same as that of M1; P3 is not as broad. Assuming that the posterior upper premolars of *E. nidhoggi* are morphologically similar to those of *E. coryphaeus*, an isolated P4 (UMVP 1475) from Purgatory Hill (V-71202) can be tentatively referred to *E. nidhoggi*. Its paracone, the highest cusp, dominates the crown and is slightly canted posteriorly. Labially a weakly developed basal cingulum
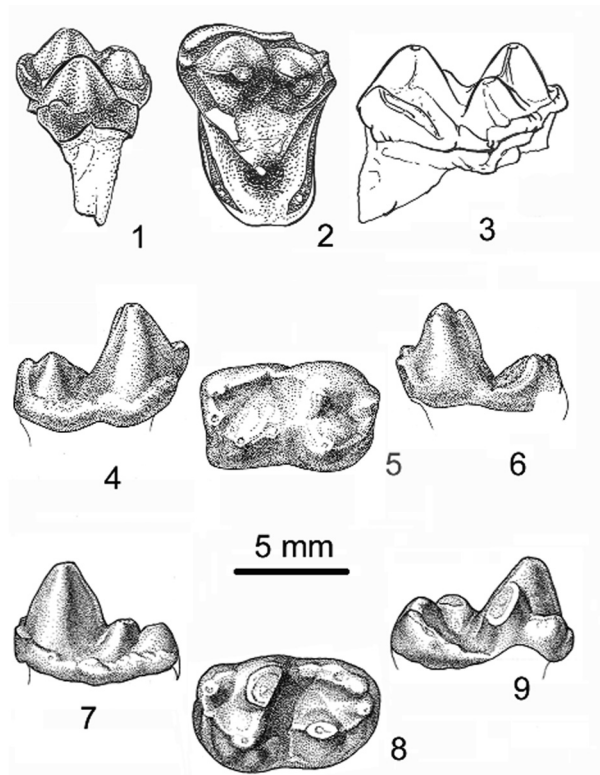
FIGURE 2. Drawings of cheek teeth of *Eoconodon nidhoggi.* UCMP 170847, left M1 or M2 in 1) lingual view; 2) occlusal view; 3) posterior view. UCMP 170848, right m2 in 4) labial view; 5) occlusal view; 6) lingual view. UCMP 145323, left m2 in 7) labial view; 8) occlusal view; 9) lingual view. (Figures 2.4-2.9 reproduced from Clemens and Williamson 2005).

links the salient parastylar region and the shorter and slightly higher metastyle. These stylar cusps are approximately the same height as the diminutive protocone. Posteriorly, a weakly developed basal cingulum extends from the metastyle to the protocone. Neither conules nor a cusp on the posterior slope of the paracone are present. The width of the crown of UMVP 1475 falls within the observed range of variation of width of isolated upper molars referred to *E. nidhoggi.*

Four isolated, damaged teeth are identified as M1s or M2s of *Eoconodon nidhoggi* (Figure 2.1-2.3). In occlusal view, the parastylar and metastylar regions are transversely broad and their margins rounded. The ectocingulum is continuous across the labial side of the crown, is of approximately the same width throughout its length, and the ectoflexus is shallow. Although the crest of the ectocingulum is slightly rugose, no distinct stylar cusps are present. The paracone and slightly smaller metacone are low bulbous cusps linked by a straight centrocrista. Anteriorly a distinct cingulum links the parastylar region with the small para-

conule. Similarly a cingulum links the metastylar region with the small metaconule. The trigon basin is shallow and ends lingually on the slope of the large protocone. The precingulum and postcingulum are distinctly developed, usually of approximately equal width, and do not meet across the lingual slope of the protocone. On one tooth (Figure 2.1-2.3) the hypoconular region of the postprotoconular cingulum is slightly expanded, but a distinct cusp is not developed.

Of the species of *Eoconodon*, only *E. coryphaeus* is known from skull fragments containing both M1 and M2 with crowns sufficiently well preserved to provide data on their length/width ratios. The morphological differences distinguishing these teeth are limited. In any specimen of *E. coryphaeus* preserving both molars, M1 is longer anteroposteriorly, and its length/width ratio is greater than that of the associated M2. Expanding the sample to include maxillary fragments preserving either M1 or M2, it becomes apparent that the ranges of variation of the length/width ratios of these molars overlap. Analysis of this expanded sample of *E.*

coryphaeus including 12 M1s and an equal number of M2s shows the range of the length/width ratio of the M1s is 0.71-0.93 (mean = 0.83); the range of the length/width ratio of the M2s is 0.65-0.87 (mean = 0 .75). On M1s of *E. coryphaeus,* the ectocingulum is divided by a shallow ectoflexus into relatively symmetrical lobes; on M2s the posterior lobe can be slightly smaller and deflected anteriorly. The differences are not great. Finally, the precingulum and postcingulum tend to be slightly broader and extend farther lingually on M1 than on M2.

Because of breakage the length/width ratio for only one of the four molars, UCMP 156110, was determinable and it (0.79) lies within the overlap of the ranges of variation of M1 and M2 of *E. coryphaeus.* As far as can be determined the ectocingulum was divided into relatively symmetrical lobes resembling M1s of *E. coryphaeus.* Differences in length and breadth of the precingulum and postcingulum are greater on molars of *E. coryphaeus* than on the isolated teeth referred to *E. nidhoggi.* Clearly, more material is needed before isolated M1s and M2s can be differentiated.

In order to provide a full description of the dentition of *Eoconodon nidhoggi,* the following descriptions, illustrations (Figure 2.4-2.9), and dimensions (Table 1) of its lower molars are reproduced from Clemens and Williamson (2005, p. 210) with emendations to account for subsequently discovered material and differences in journal format.

Three fragmentary m1s are referable to *Eoconodon nidhoggi.* Their protoconids and slightly lower metaconids are separate cusps only in the upper one-third of the trigonid. The paraconid, distinctly lower and projecting anteriorly, is situated in front of the base of the notch in the protocristid. Differing from m1s of *E. gaudrianus* and the new species described below, the labial basal cingulid is continuous along the entire length of the tooth. The hypoconid is the largest and highest talonid cusp. Hypoconulid and entoconid are subequal in height and closely approximated to form a transverse ridge. The entocristid extends to the back of the trigonid but decreases in height anteriorly so the trough-like talonid basin opens lingually behind the metaconid. The two roots are of approximately equal size.

Morphologically m1s and m2s of *Eoconodon nidhoggi* only differ slightly in that the paraconid of m2 is less salient anteriorly and situated slightly labial to the metaconid, not in front of the notch in

the protocristid (Figure 2.4-2.6). The labial basal cingulid is not as strongly developed as it is on m1.

The last molar is known from the type specimen of *Eoconodon nidhoggi* (UMVP 1471) and two other isolated teeth (Figure 2.7-2.9). Comparisons of isolated m2s and m3s suggest that in any individual m3 might have been slightly longer (Table 1). In comparison to m2s the trigonid of m3 is slightly lower relative to the height of the talonid. The protoconid is more robust and slightly higher than the metaconid. On m3s the paralophid extends anterolingually down the protoconid and then turns to reach the small paraconid. On the type the labial basal cingulid is interrupted on the posterolabial side of the trigonid. On the referred molars this cingulid begins below the paraconid and continues as a narrow shelf across the trigonid and talonid before rising to end at the base of the hypoconulid. As on other molars, the hypoconid of m3 is the largest talonid cusp and linked to the slightly lower hypoconulid by a strong ridge. The entoconid is distinctly smaller and separated by a groove from the hypoconulid. Extending anteriorly from the entoconid, the entocristid decreases in height and ends at the lingual side of the base of the metaconid. Just posterior to the metaconid the talonid basin is broadly open lingually across the low entocristid. Of the two roots, the posterior is significantly larger and directed posteroventrally. Unlike m3s of *E. gaudrianus* from the San Juan Basin, the back of the hypoconulid is more vertically oriented and separated from the root by a distinct notch.

Eoconodon hutchisoni new species

Holotype. UCMP 156108, a left M2 preserved in a fragment of maxillary.

Type Locality. UCMP V81028, Tullock Formation, Garfield County, northeastern Montana, Pu2/Pu3.

Hypodigm and localities. ?DP3 or **DP4**, UCMP 145677 (V-73080); **P4**, LACM 28140 (V-72125), UCMP 170844 (V-73080), UCMP 156102, 156118 (V-73082); **M1**, UCMP 156100, 156104 (V-73080), UCMP 156120 (V-73096); **M2**, UMVP 1450 (V-71202), UCMP 156103 (V-72130), UCMP 156105, 156106, 170845, 186684 (V-73080), UCMP 156108 (V-81028); **M3**, UCMP 156109 (V-72130), UCMP 170846 (V-73080), UCMP 156119 (V-74123); **p4**, UCMP 145676, 156112, 156113, 156114, 156115, 170869 (V-73080); **m1**, UCMP 145324 (V-72130), UCMP 110515, 192011, 192012 (V-73080), UCMP 110590, 192016 (V-73096); **m2**, LACM 28138 (V-72125), UCMP 110516, 145326, 145327, 145333, 192013 (V-

73080), UCMP 156117 (V-75196); **m3**, LACM 28139 (V-72125), UCMP 156116 (V-72131), UCMP 145331 (V-73080), UCMP 192017 (V99438); **casts of two fragments of a dentary**, one containing m2-3, the other preserving part of the symphyseal region, UCMP 124393 (V-80002).

All of the following UCMP localities are in Garbani Channel deposits either at the main quarry locality or elsewhere in the western headwaters of Cottonwood Creek (see Archibald 1982): V-72125, V-72130, V-72131, V-73080, V-73082, V-73096, V-74123, V-81028, and V-99438. Additional specimens of *E. hutchisoni* have been found at Purgatory Hill (UCMP loc. V-71202), Kerr Butte (UCMP loc. V-75196, see Archibald 1982, p. 33-34), and a locality somewhere in the valley of Hell Creek (V-80002) discovered by Reverend Wayne Moore.

Etymology. Named to recognize the many contributions to vertebrate paleontology made by Dr. J. Howard Hutchison. The type specimen is just one of a multitude of fossils that he discovered and that significantly add to the basis of research on the faunas of the Hell Creek and Tullock Formations of northeastern Montana.

Diagnosis. Postcanine dentition of *Eoconodon hutchisoni*, where known, is smaller than that of *E. coryphaeus* or the observed ranges of variation slightly overlap (Table 1). Its postcanine dentition is larger than those of *E. nidhoggi* and *E. ginibitohia* but again a few observed ranges of variation slightly overlap. With the exception of the distinctly smaller p4s and m3s of *E. hutchisoni*, the other lower postcanines in the small sample of *E. gaudrianus* are either slightly smaller than or within the lower end of the observed range of variation of those of *E. hutchisoni*.

The P4 of *Eoconodon hutchisoni* differs from that of *E. gaudrianus* and the P4 tentatively referred to *E. nidhoggi* (UMVP 1475) in its significantly larger protocone that, particularly in comparison to *E. gaudrianus,* is more distinctly separated from the base of the paracone. P4s of *E. hutchisoni* have a small, metacone-like expansion on the posterior slope of the paracone, which is lacking in *E. gaudrianus*, and possibly *E. nidhoggi,* and the posterior margin of the ectocingulum is more rugose. Differing from M1s or M2s of *E. nidhoggi* in which the metacone is slightly smaller than the paracone, on M1s of *E. hutchisoni* these cusps are subequal while on M2s the metacone is the smaller cusp. On M1s of *E. hutchisoni* the postcingulum is broader than that of the M1s or M2s of *E. nidhoggi* and has a distinct hypocone. The metacone of M3 is much smaller than the paracone. A metaconule

is present but the paraconule is either small or missing. Its trigon basin is divided by a low transverse crest. Precingulum and postcingulum are narrow and do not meet on the lingual face of the protocone.

The protoconids of p4s of *Eoconodon hutchisoni* are not as distinctly canted posteriorly as those of *E. gaudrianus,* and, particularly, *E. coryphaeus.* The lengths of the m1s and m2s of *E. hutchisoni* are smaller than those of *E. coryphaeus*, greater than those of *E. nidhoggi* and *E. ginibitohia*, and overlap with those of *E. gaudrianus* (Table 1). In contrast to the other currently recognized species, the m3 of *E. hutchisoni* is distinctly shorter and narrower than m2. (Based on means, see Table 1, the crown length of m3 is 86% of that of m2 and the trigonid width of m3 is 84% of that of m2.) The m3 talonid is reduced in size relative to the trigonid, and on one specimen the talonid cusps are reduced to crenulations around the talonid basin. On m3s of *E. hutchisoni* the posterior slope of the hypoconulid is separated from the posterior root by a distinct notch, while in *E. gaudrianus* (e.g., AMNH 3400 and the fragmentary m3 of AMNH 58116) the posterior slope of the hypoconulid merges smoothly with the surface of the enlarged posterior root.

Description and comparisons. The majority of the specimens forming the available sample of *Eoconodon hutchisoni* are isolated teeth. One of two exceptions is UCMP 156108, the type specimen, which consists of an M2 preserved in a fragment of maxillary including the posterior walls of the alveoli of M1, the anterior walls of alveoli of M3, and the anterior base of the zygomatic arch. The other is UCMP 124393, which consists of two, very probably associated, fragments of a dentary. One contains both m2 and m3. The other preserves the symphyseal region. Identifications of the positions of the postcanines of *E. hutchisoni* not represented in these specimens are based on comparisons with the dentitions of other species of *Eoconodon*, primarily *E. coryphaeus*.

UCMP 145677 (Figure 3.1-3.2) is tentatively referred to *Eoconodon hutchinsoni* on the basis of its large size (length = 6.95 mm; width = 5.20 mm) and bulbous morphology of the paracone. Its three well-separated roots are of approximately equal size and divergent suggesting this tooth is a DP3 or DP4. In occlusal view, the broad, rounded parastylar region is salient and bears a distinct parastylar cusp. The posterior crest of the relatively low paracone extends to a posterior accessory cusp on the broader metastylar region. A distinct basin,
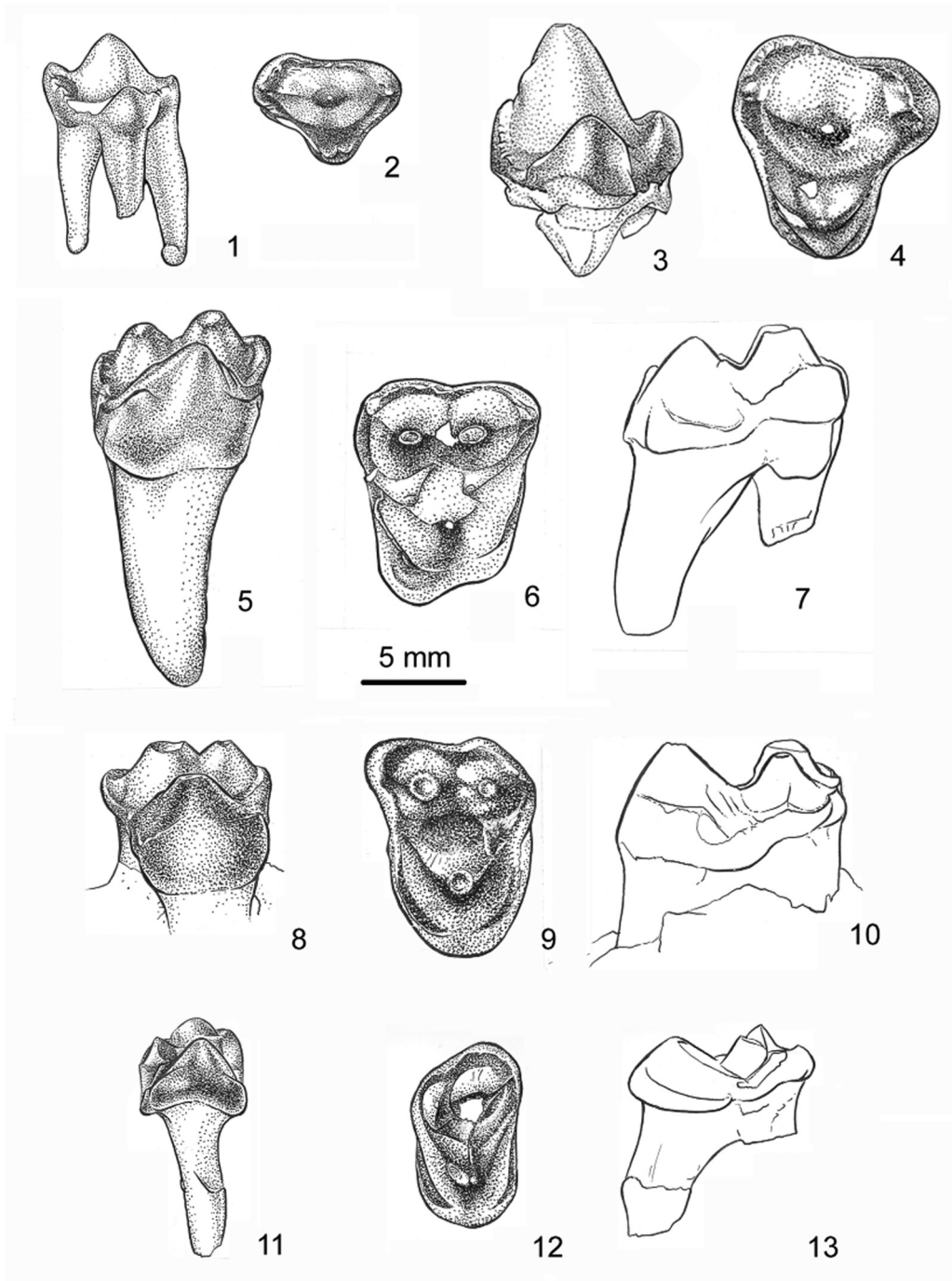
FIGURE 3. Drawings of upper cheek teeth of *Eoconodon hutchisoni*. UCMP 145677, right ?DP3 or DP4 in 1) lingual view; 2) occlusal view. LACM 28140, right P4 in 3) lingual view, 4) occlusal view. UCMP 156104, right M1 in 5) lingual view, 6) occlusal view, 7) posterior view. UCMP 156108, holotype, left M2 in 8) lingual view, 9) occlusal view, 10) posterior view. UCMP 156109, right M3 in 11) lingual view, 12) occlusal view, 13) posterior view

developed labial to this crest, is the terminus of the narrow, crenulated ectocingulum. The small protocone is linked to base of paracone by a low, indistinct crest and to the parastylar and metastylar regions by narrow basal cingula.

In occlusal view, the parastyle of the P4 is large, rounded, and anteriorly projecting (Figure 3.3-3.4). Viewed laterally, the anterior crest of the high paracone is longer than the posterior, which carries a small metacone-like expansion and termi-

nates in a small posterior accessory cusp. Above the apex of the paracone, the ectocingulum narrows to a faint ridge. Posteriorly it expands onto the anteroposteriorly short but broad metastylar region. The prominent protocone is linked to the paracone by a low, rounded surface delimited anteriorly and posteriorly by traces of cingula extending from the protocone to the parastylar and metastylar regions. Conules are lacking. A small postcingulum is present on one (LACM 28140) of the three specimens preserving this region. The three roots are of approximately equal size and not divergent.

The salient, rounded parastylar region of M1 carries a small, distinct cusp (Figure 3.5-3.7). A very shallow ectoflexus divides the ectocingulum into symmetrical lobes. Usually a small mesostylar cusp is present. Paracone and metacone are low, conical cusps of essentially equal size. Low ridges extend from the paraconule and metaconule toward the bases of the paracone and metacone. A preparaconule crista extends to the parastyle; the postmetaconule crista extends to the posterior labial corner of the crown. The areas between the conules, paracone, and metacone delimited by these crests are essentially flat surfaces. The labial side of the high protocone is also relatively flat. The trigon is essentially an antero-posteriorly oriented trough, not a basin. It consists of the two flat areas labial to the conules and the flat but more dorsally placed labial surface of the protocone. A narrow precingulum is present. The posterior slope of the protocone is inflated, and bears a postcingulum that terminates lingually in a small hypocone. On M1s and other upper molars irregular bumps and nearly vertical striae can be present particularly on the near vertical, lingual surfaces of the cusps. Of the three roots, the lingual is much greater in length and diameter at base of crown than the other two.

The M2s are more transversely broadened than M1s, which is reflected in their length/width ratios (M2, 0.72-0.76 vs. M1, 0.83). In occlusal view (Figure 3.8-3.10), the labial margin of the ectocingulum is asymmetrical with the posterior lobe slightly deflected anteriorly. Unlike M1s the paracone of M2s is somewhat larger than the metacone. Also the trigon is shallowly but distinctly basined. Differing from M1s, the precingulum and postcingulum are of approximately equal width and lack a hypocone. These cingula usually do not meet across the labial face of the protocone, but on two of the six teeth there is a narrow connection. Of the three roots, the lingual is largest and longest.

On the basis of their large size and bluntly conical cusps three isolated M3s are referred to *Eoconodon hutchisoni*. On these teeth the ectocingulum extends around the not greatly expanded parastylar region (Figure 3.11- 3.13). A very small parastylar cusp is situated lingually and connected to the paracone by a low crest. Posterolabially, the ectocingulum is continuous; its crest is crenulated but distinct stylar cusps are not developed. The paracone is much larger than the metacone. A small metaconule is present. On one tooth a smaller paraconule is present; the others lack this cusp. The morphology of the trigon varies. On one tooth (UCMP 156109), a distinct transverse ridge divides the trigon into anterior and posterior basins. Its precingulum and postcingulum are well developed but do not meet lingually. On the other referred teeth the trigon basins are smaller. Their occlusal surfaces are slightly convex but lack a pronounced transverse crest. The precingulum and postcingulum are short and poorly defined. The crown was supported by two roots; the lingual is slightly larger.

When viewed laterally, the protoconid of p4, the dominant cusp, is slightly canted posteriorly with its anterior slope convex and the posterior nearly straight (Figure 4.1-4.3). It is not as posteriorly canted as the protoconids of *Eoconodon gaudrianus* and particularly *E. coryphaeus*. A small anterior accessory cusp is present. There is no indication of a metaconid. An extension of the posterior crest of the protoconid forms the labial edge of a shallowly basined talonid and terminates at the hypoconulid. The hypoconulid is flanked by a labial cusp of approximately equal height and a lingual crest, which can carry a small cusp. Of the two roots the posterior is more robust.

The protoconid and slightly lower metaconid of m1 are separate cusps only in approximately the upper one-third of the trigonid (Figure 4.4-4.6). The paraconid is distinctly lower, is situated in front of the notch separating the protoconid and metaconid, and projects anteriorly. A broad anterior basal cingulid extends ventrolabially from the base of the paraconid to the base of the trigonid, narrows or is interrupted across the labial face of the trigonid, continues posteriorly across the labial face of the talonid, and then turns dorsally to end at the base of the hypoconulid. The hypoconid is the largest and highest talonid cusp. Hypoconulid and entoconid are subequal in height and closely approximated to form a transverse ridge (postcristid). From the entoconid, the entocristid decreases in height toward the trigonid allowing the trough-
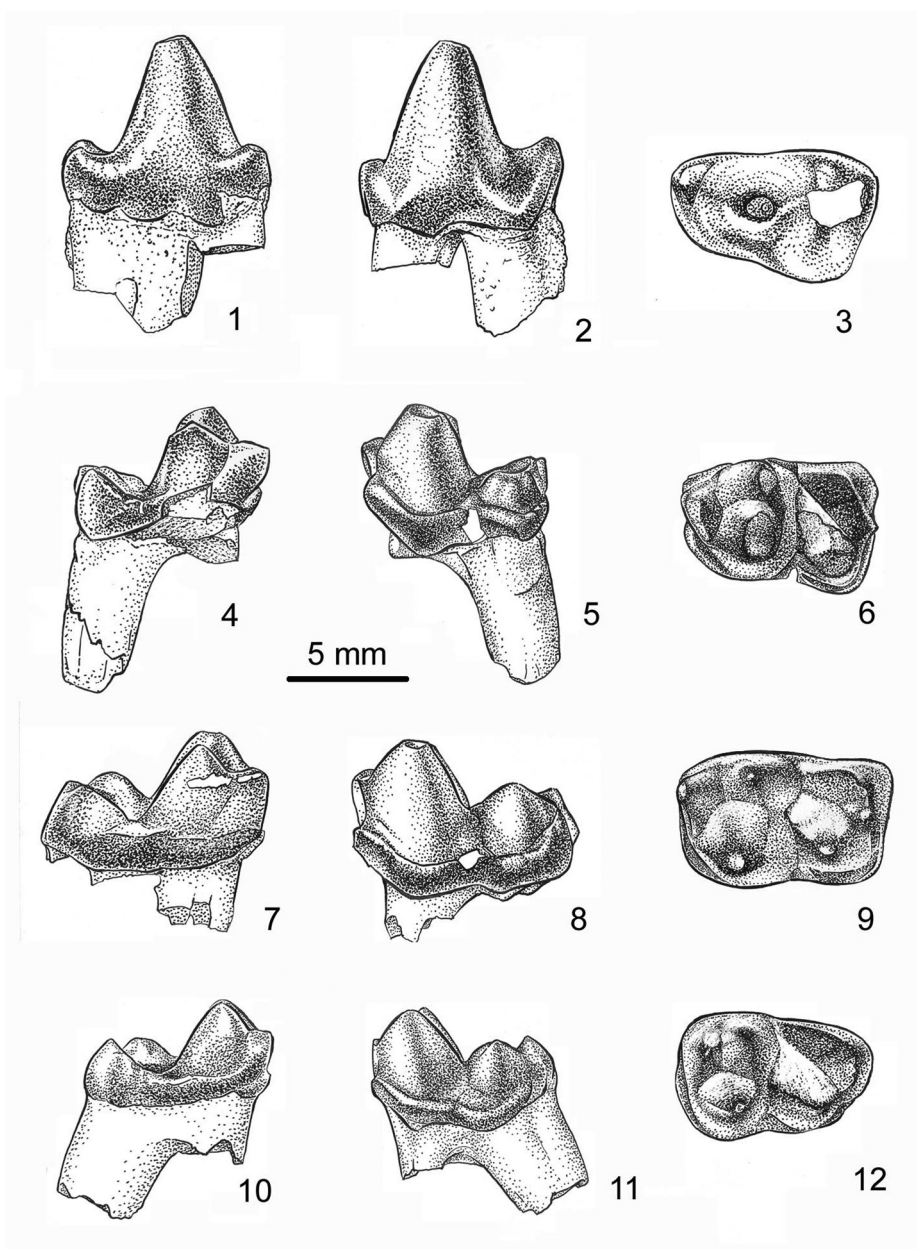
FIGURE 4. Drawings of lower cheek teeth of *Eoconodon hutchisoni*. UCMP 156115, right p4 in 1) lingual view, 2) labial view, 3) occlusal view. UCMP 110515, right m1 in 4) lingual view, 5) labial view, 6) occlusal view. UCMP 156117, right m2 in 7) lingual view, 8) labial view, 9) occlusal view. UCMP 145331, right m3 in 10) lingual view, 11) labial view, 12) occlusal view.

like talonid basin to open lingually behind the metaconid. The two roots are of approximately equal size.

The m2s differ slightly from m1s in that the paraconid is not as salient anteriorly, usually is more lingually situated, and the apices of para-conid and metaconid are more closely approximated (Figure 4.7-4.9). In *Eoconodon coryphaeus*, whose lower dentition is known from a large num-ber of specimens (Table 1), the length of m1 tends to be slightly shorter than that of m2. Also, the width of the m1 trigonid is less than that of the tal-onid, while on m2 the trigonid is slightly wider than the talonid. These proportions, which describe the m2 preserved in a fragment of dentary (UCMP 124343), have been used to distinguish isolated m1s and m2s of *E. hutchisoni*.
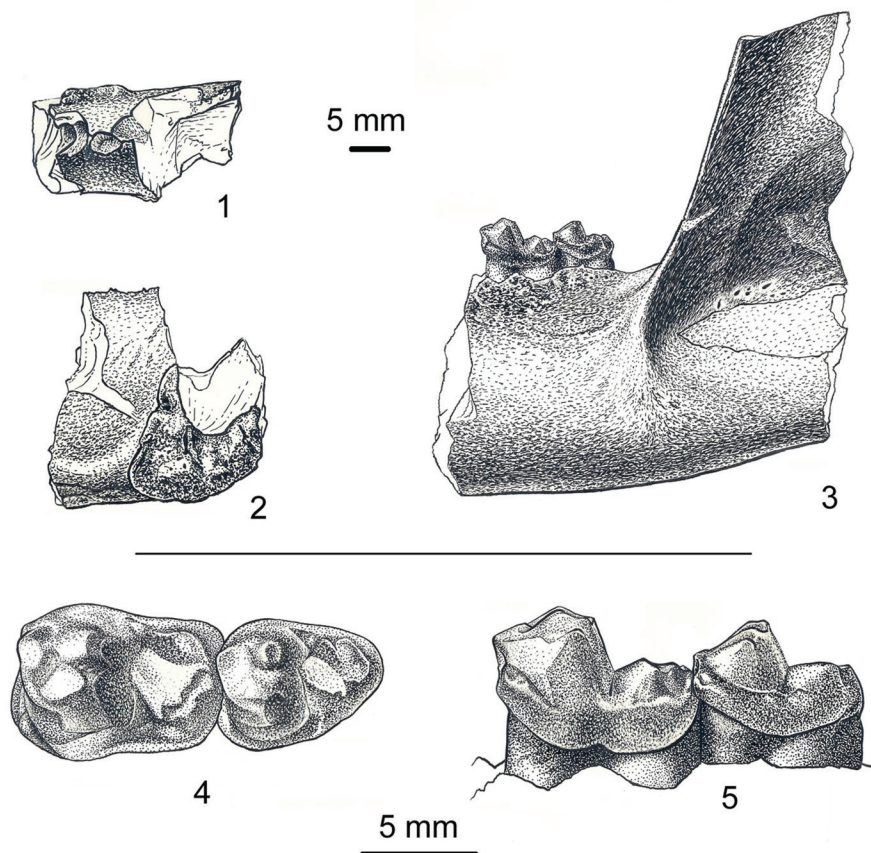
FIGURE 5. Drawings of two fragments of a dentary of *Eoconodon hutchisoni,* UCMP 124398. Fragment of the symphyseal region of the dentary in 1) dorsal view, symphysis at lower right, 2) internal view showing symphyseal surface in the lower right. Fragment of mandibular ramus containing m2-m3 in labial view. Enlarged drawings of m2-m3 in 4) occlusal view, 5) labial view.

The protoconid of m3 is more robust and slightly higher than the metaconid; the paraconid is distinctly smaller and, unlike m1 and m2, situated directly in front of the metaconid (Figure 4.10-4.13). The talonids of most m3s resemble those of the other molars in that the hypoconid is the largest talonid cusp, and the slightly smaller hypoconulid is linked to the entoconid by a strong ridge (postcristid). On one tooth (UCMP 192017) the talonid basin is rimmed by a series of small cusps whose homologies are not apparent. The talonid is much narrower than the trigonid, although the degree of its diminution relative to the trigonid is variable. The labial base of the crown is expanded, and on some teeth a cingulid is present on the anterior face of the trigonid and labial side of the talonid. Of the two roots the posterior is separated from the crown by a shallow notch around the top of the root, significantly larger, and directed posteroventrally,

Two fragments of a dentary were discovered by Reverend Wayne Moore and made available for casting (UCMP 124393) and study. Although a contact between the two fragments is lacking, their reported discovery in the same small area as well as similarities in size and mode of preservation indicate they are most probably elements of the same dentary (Figure 5). Unfortunately I was not able to revisit the locality where they were discovered, which was described as being in the valley of Hell Creek near the road to the Hell Creek Recreation area. This road passes through outcrops of the Tullock Formation that are assumed to include the source of the fossil.

One fragment of UCMP 124393 includes parts of the symphyseal region, the alveolus for the canine, and alveoli for two, two-rooted premolars (Figure 5.1-5.2). Depth of the dentary below the premolars is ca. 2.8 cm, which is comparable to

that of the posterior fragment. The positions of the premolar alveoli suggest the anterior two premolars were crowded and set en echelon with their posterior roots lingual to the anterior. There is no evidence of mental foramina on what remains of the labial side of the dentary. Medially, what remains of its rugose surface indicates the symphysis was massive. The posterior edge of the symphysis is rounded and, ventrally, projects posteriorly. From this projection a low but distinct ridge extends posteriorly, parallel to the bottom of the dentary. The second fragment consists of part of the posterior end of the dentary including the nearly vertical anterior edge of the coronoid process as well as m2 and m3 (Figure 5.3). The masseteric fossa is sharply delimited anteriorly. On the lingual side of the dentary a horizontal ridge is present ventral to the coronoid process and ca. 8 mm below the alveolar level of the ramus.

Two fragmentary dentaries of *Eoconodon gaudrianus* (AMNH 3400 and 58116) are smaller than but resemble UCMP 124393 in their similar depth throughout their length and heavily built symphyses. Dentaries of *E. coryphaeus* exhibit a similar massive structure. On most specimens of *E. coryphaeus* the anterior part of the dentary is absent or poorly preserved. Where it is present usually there is no evidence of crowding of the premolars. In contrast, the anterior part of the dentary of AMNH 16333 preserves the root of the canine and parts of the crowns of p1-2 and the complete p4 as well as m1-2. The large canine is separated from p1 by a short (ca. 4.0 mm) diastema, which is the only significant gap in the postcanine dentition. The damaged crown of p1 had a smaller diameter than its single root. A thin interalveolar wall, ca. 0.5 mm, separates the roots of p1 and p2. Three roots support p2, the larger anterior and posterior roots and a smaller, labial root below the apex of the main cusp. The p2 and p3 are set en echelon with p3 overlapping the labial side of p2 by ca. 2 mm, which is the only observed occurrence of crowding in the premolar dentition of *E. coryphaeus*.

In an early study of the enamel microstructure of Paleocene mammals, Koenigswald et al. (1987) described the structural complexity of the enamel of *Eoconodon coryphaeus* (identified as *E. heilprinianus*) and *E. gaudrianus*. They reported organization of the enamel prisms into groups following divergent paths outward from the enamel-dentine junction creating Hunter-Schreger bands. When a tooth is viewed laterally or in tangential section primitively Hunter-Schreger bands are approximately parallel and relatively straight. In more

derived structural patterns the bands are undulating culminating in a zig-zag pattern, which increases the resistance of the enamel to splitting (see Stefen 1997a, 1997b). Stefen (1999) examined sections through the trigon of UC 156100, now identified as an M1 of *E. hutchisoni,* and a fragment of another upper molar, UCMP 171513, of this species. In these specimens the Hunter-Schreger bands exhibit an increasing degree of waviness from the base toward the apex of the crown. Currently species of *Eoconodon* provide the earliest record of this derived microstructural pattern in eutherian mammals (Stefen 1999).

Comments. Determination of the generic reference of *E. hutchisoni* highlights the current limitations of the definitions and diagnoses of *Eoconodon* and *Goniacodon*, which is known from Pu3 and Torrejonian faunas in the Western Interior, primarily the San Juan Basin, New Mexico, and Dragon Canyon, Utah (Lofgren et al. 2004). Matthew (1937) reviewed *Goniacodon* and its type species, *G. levisanus,* and cited several dental and mandibular characters distinguishing it from *Eoconodon*. Upper molars are less quadrate – considerably wider than long – than those of *Eoconodon.* M1 is as large as or larger than M2; the proportions of these molars in *Eoconodon* are reversed. Protoconules are absent but metaconules are distinct. In *Goniacodon*, hypocones are present on M1-2. Paraconids of the lower molars are relatively smaller than those of the molars of *Eoconodon*. Protoconid of p4 of *Goniacodon* is "…rather recurved towards the tip than backwardly pitched from the base (Matthew 1937, p. 88)" as is the case in *Eoconodon*. The mandibular symphysis of *Goniacodon* was described as "…ovate and widest behind extending back to beneath the third premolar while in *Eoconodon* it is widest anteriorly and pointed behind" (Matthew 1937 p. 86). In *Goniacodon*, the mental foramina are positioned far forward below p1 and p2. The M3 and m3 were described as "reduced" (Matthew 1937, p. 86) or "much reduced" (Matthew 1937, p. 87) in comparison to the second molars. As is the case with molar proportions, quantitative data were not given.

In almost all of the characters cited by Matthew (1937) *E. hutchisoni* resembles other species of *Eoconodon* and not *Goniacodon,* which appears to have more derived character states. An exception is the reduction in relative size of m3 of *E. hutchisoni* (M3 of this species has yet to be identified). In the fragmentary mandible of *E. hutchisoni* (UCMP 124393) the length of m3 is 83% of that of

m2; trigonid width of m3 is 82% of that of m2. Adding isolated teeth, the mean values of length and trigonid widths of m3s are, respectively, 86% and 84% of those of m2s. Where known, the m3s of other species of *Eoconodon* are approximately the same size as their m2s. Dimensions of m2 and m3 of *G. levisanus*, supplied by Thomas Williamson (personal commun., 2007), indicate that the mean length of m3s in this species is approximately 70% of the mean length of m2s, and mean trigonid width of m3s is 68% of that of m2s. Although the length and trigonid width of m3 relative to those of m2 of *E. hutchisoni* are smaller than in other species of *Eoconodon,* they are not as greatly reduced as in *Goniacodon levisanus.*

Eoconodon copanus Van Valen, 1978

Type. PU 13290, left m1? (Jepsen 1930, Plate IV, Fig. 5)

Type locality. Mantua Lentil, Polecat Bench Formation, Wyoming (Jepsen 1930; Van Valen 1978)

Diagnosis. "Lower molars elongate, entoconid small and distal. Same as *Eoconodon* sp. of Jepsen (1930, Plate IV, fig. 5) $M_{?1}$ l, 10.4, trd w, 5.6, tald w, 5.4 (Van Valen 1978, p. 57)" .

Comments. The type and only specimen of *Eoconodon copanus* (PU 13290) is from the sample of the early Puercan (Pu1) Mantua local fauna. Its salient paraconid suggests that the tooth is an m1. A fracture extends diagonally along the floor of the trough-like, lingually-sloping talonid basin. The part of the talonid containing both the entoconid and hypoconulid is shifted slightly distally. Some separation of the fragments has occurred and could influence the measurements of length of the crown and width of the talonid.

Dimensions measured on a cast of PU 13290 (Table 1) differ somewhat from those reported by Van Valen (1978). Depending upon which set of measurements of PU 13290 is used, its crown length falls just within the lower limit of the observed range of variation of *Eoconodon coryphaeus* or between that and the observed range of variation in the smaller *E. hutchisoni.* Both of the measurements of its trigonid width are distinctly smaller than those of *E. coryphaeus.* The measurement reported by Van Valen (1978) falls just within the lower bound of the observed range of variation of *E. hutchisoni*; the measurement based on the cast is smaller. Both sets of measurements indicate that the talonid of PU 13290 is narrower than the talonids of m1s of *E. coryphaeus* and *E. hutchisoni.* This relative narrowness of the crown of PU 13290 reflects the lack of expansion of the base of the crown and development of distinct basal cingulids that characterize the m1s and m2s of *E. hutchisoni* and *E. coryphaeus*.

Van Valen (1978) cited the small size and distal position of the entoconid in his diagnosis of *Eoconodon copanus*. The entoconid is small but, in comparison to the talonid cusps of other species of *Eoconodon,* it is not particularly reduced, and its position is not greatly different from that in *E. nidhoggi* and *E. hutchisoni.* Until a larger sample is discovered, the relative narrowness of the crown and its length – approximately intermediate between those of m1s of *E. nidhoggi* and *E. hutchisoni* – warrant continued recognition of *E. copanus* as a distinct species.

Eoconodon sp.

Numerous fossil localities in a remarkably thick (over 530 m, Eberle and Lillegraven 1998a) and structurally uncomplicated section of the Ferris Formation in the Hanna Basin, south central Wyoming, have yielded remains of Lancian and Puercan (Pu1 through Pu3) mammals. Eberle and Lillegraven (1998b) documented the presence of *Eoconodon* in the Pu1 and Pu2 interval zones. The Pu1 record is based on an isolated right upper molar (UW 26187), probably an M2. Eberle and Lillegraven (1998b, p. 102) noted that this molar is about half the size of homologous molars of *E. coryphaeus* and somewhat smaller than those of *E. gaudrianus* and "…the unnamed larger species from Purgatory Hill…" (=*E. hutchisoni*). Basing an estimate of the sizes of its upper molars on the dimensions of the type of *E. nidhoggi*, an m3, they suggested that UW 26187 probably was smaller than the upper molars of *E. nidhoggi*. Although few in number, the sample of M1s or M2s of *E. nidhoggi* described above fully supports their estimate. Also, the molars of *E. nidhoggi* differ in the similar length and width of their precingulum and postcingulum and the absence of a distinct hypocone. Again based on an estimate of size of the upper molars of *E. copanus*, Eberle and Lillegraven (1998b) argued that UW 26187 probably is too small to be referable to this species, the only Pu1 species of *Eoconodon* currently recognized and named.

The second specimen of *Eoconodon* from the Hanna Basin, found at a Pu2 locality, is a fragment of the labial part of an upper molar (UW 26221), which, as far as can be determined, resembles UW 26187. Eberle and Lillegraven (1998b) suggested that the two specimens from the Ferris Formation represent a new species of *Eoconodon.* With discovery of larger samples, it would be appropriate to

compare *Eoconodon* sp. from the Ferris Basin with *E. ginibitohia* (Clemens and Williamson 2005) from the San Juan Basin, which is the smallest, currently named species of the genus.

Although small, the records of *Eoconodon* from the Ferris Formation are significant in documenting the presence of a second species of the genus in Pu1 faunas of the Western Interior. Although the collections from Pu3 localities are described as quite large consisting of "hundreds" of mammalian specimens (Eberle and Lillegraven 1998b, p. 110), a record of *Eoconodon* or another "triisodontid" is lacking.

DISCUSSION

Phylogenetic Hypotheses

McKenna and Bell (1997) included the North American Paleocene genera *Goniacodon, Eoconodon, Triisodon,* and *Stelocyon,* as well as the Asian Eocene *Andrewsarchus* in the Family Triisodontidae. In subsequent phylogenetic analyses "triisodontids" often were represented by only two genera, *Eoconodon* and *Andrewsarchus* (e.g., Geisler and McKenna 2007). In some analyses, these two genera were found to be relatively closely related, but inclusion of *Andrewsarchus* in a monophyletic Triisodontidae was frequently challenged (see O'Leary et al. 2003 and references cited therein). Similarly, interpretations of the phylogenetic relationships of *Eoconodon* have varied widely. In some studies, the genus was interpreted as very distantly related to the Cetartiodactyla and allied with, for example, the archaic ungulate *Arctocyon* or the late Eocene to late Oligocene leptictid *Leptictis* (e.g., O'Leary and Geisler 1999).

Williamson and Carr (2007) undertook an analysis of the phylogenetic relationships of basal ungulates and basal mesonychians directed toward testing hypotheses of the phylogenetic interrelationships of "triisodontids" (*Eoconodon, Goniacodon,* and *Tricentes*), *Oxyclaenus, Microclaenodon,* and mesonychians. In this study they considered only species of *Eoconodon* (*E. coryphaeus, E. gaudrianus,* and *E. ginibitohia*)*, Goniacodon* (*G. levisanus, G. crassicuspis,* and *G. hiawathae*)*,* and *Tricentes* (*T. quiverensis*) known from the San Juan Basin and other southern localities. The northern species of *Eoconodon* (*E. copanus, E. nidhoggi,* and *E. hutchisoni*) were not considered. Their analysis, which is followed here, demonstrated that "triisodontids" are a paraphyletic group. It was inconclusive in clarifying the interrelationships of the species of "triisodontids" yielding a polytomy including the three southern species of *Eoconodon*, a lineage composed of three species of *Goniacodon* and the *Triisodon quiverensis* lineage.

Paleobiogeography

Eoconodon is unknown in Lancian faunas but the genus is a member of Puercan and early Torrejonian faunas of the Western Interior and possibly Texas. The samples of these faunas come from sites with different depositional and, most likely, taphonomic histories. They represent the fruits of different collecting techniques ranging from surface collecting to underwater screening. As emphasized by Lofgren et al. (2005) these differences in sampling must be considered in any paleobiogeographic study.

Lancian North American Land Mammal Age. Biochronologically the boundary between the Lancian and Puercan is defined by the first appearance of the archaic ungulate *Protungulatum* and approximates but is not always coeval with the Cretaceous/Tertiary boundary. In contrast, the base of the Lancian is not well defined (Cifelli et al. 2004). Wilson (2005) suggested that the ages of the Lancian local faunas in northeastern Montana fall within the last 1.8 m.y. of the Cretaceous. Lancian faunas from other areas are not as well constrained temporally and might well include some that are older (Cifelli et al. 2004).

Geographically, large samples of Lancian local faunas have been made from sites in both overbank and channel lag deposits discovered in Colorado, Wyoming, Montana, North and South Dakota, and northward into Saskatchewan and Alberta (Figure 1 and, Cifelli et al. 2004., Figure 2.2). To the south a few hard won Lancian fossils have been recovered in the Dragon Canyon area, Utah, (Cifelli et al. 1999) and the San Juan Basin, New Mexico (Weil and Williamson 2000).

Remains of *Eoconodon* have not been discovered in any Lancian vertebrate fossil locality within the Western Interior. Some of these samples amassed through underwater screening at localities in the northern Western Interior are very large. For example UCMP collections from the two primary collecting localities in channel lag deposits within the Lance Formation, Wyoming (UCMP V-5620 and V-5711) include 3,249 cataloged mammalian specimens (UCMP online database). UCMP collections from Lancian localities in the Hell Creek Formation, Montana, include 1,471 cataloged mammalian specimens obtained from both overbank and channel lag deposits (Wilson 2005).

Many of these collections include molars of *Didelphodon vorax*, which are only slightly smaller than the morphologically similar molars of the smallest known species of *Eoconodon*. Although non-tribosphenic in morphology, isolated molars of Lancian multituberculates rival the size of those of the smaller species of *Eoconodon.* It is unlikely that the absence of cheek teeth of *Eoconodon* from these collections is a product of hydrodynamic sorting favoring smaller fossils. In summary, given their geographic distribution, derivation from both overbank and channel deposits, and large size of some of the currently available samples, the lack of specimens of *Eoconodon* probably documents its absence from at least the northern Western Interior during the Lancian.

Early Puercan, Pu1 interval zone. The beginning of the Pu1 interval zone is defined by the first occurrence of *Protungulatum*; its end by the first occurrence of *Ectoconus* (Lofgren et al. 2004). At localities where the magnetostratigraphy can be clearly determined, all Pu1 local faunas are preserved in sediments deposited during magnetic polarity chron C29r. Radiometric age determinations of deposits in the Western Interior provide an age of 65.58 ± 0.04 m.y. for the Cretaceous/Tertiary boundary, which is within chron 29r; the age of the boundary between chrons C29r and C29n is taken at 65.16 m.y. (Wilson 2005). Thus the duration of the Pu1 interval zone is on the order of 420,000 years.

The geographic distribution of fossil localities yielding Pu1 mammalian local faunas is heavily biased in favor of the northern Western Interior. Pu1 local faunas have yet to be discovered in either the San Juan Basin, New Mexico, or the Dragon Canyon area, Utah. Currently, the southernmost Pu1 local fauna is the Littleton local fauna from the Denver Basin, Colorado (Middleton and Dewar 2004). Here and at the Pu1 Mantua locality, Big Horn Basin, Wyoming, most of the material was obtained through surface collecting and hand quarrying. Pu1 localities in the Hanna Basin, Wyoming, were sampled with these and screen-washing techniques. Two localities in Saskatchewan, Frenchman 1, and Long Fall have yielded samples of local faunas that appear to contain a mixture of Lancian and Pu1 mammals. Provisionally they have been interpreted as being of Pu1 age (Lofgren et al. 2004).

The largest samples of Pu1 local faunas and time-averaged (Lancian and Pu1) Bug Creek Assemblages come from the uppermost Hell Creek and basal Tullock Formations in northeastern Montana. Archibald's (1982) study of the Pu1 Hell's Hollow local fauna in Garfield County, Montana, was based on 717 mammalian specimens (UCMP online database) obtained primarily by screen washing. The Bug Creek Assemblage, known primarily from large channel fillings in western McCone County, Montana, is a time-averaged accumulation of both Lancian and Pu1 vertebrate fossils deposited during the Pu1 interval zone (Lofgren 1995). The exuberantly productive Bug Creek Anthills and other sites in the valley of Bug Creek have yielded thousands of mammalian specimens. Sloan and Van Valen (1965), for example, reported that after 10 weeks of field work about 27,000 mammalian teeth and fragmentary jaws had been collected at the Bug Creek Anthills locality, and they presented an analysis of taxonomic diversity based on 6,000 specimens. Sites in the McGuire Creek area to the south of the valley of Bug Creek yielding the Bug Creek Assemblage produced approximately 3,000 mammalian specimens that were analyzed by Lofgren (1995).

Eoconodon is not represented in any of the large samples of Pu1 faunas or Bug Creek Assemblage localities found in northeastern Montana. Given the immense size of these collections the lack of specimens referable to *Eoconodon* probably reflects its absence from the area. As currently known, occurrences of *Eoconodon* in Pu1 local faunas are limited to two sites in Wyoming. *Eoconodon copanus* is typified on an isolated molar in the sample of the Mantua local fauna, Polecat Bench Formation (Van Valen 1978). Eberle and Lillegraven (1998b) reported the presence of *Eoconodon* sp. in the Hanna Basin (Ferris Formation), Wyoming, based on an isolated upper molar that most likely is not referable to *E. copanus*.

It remains an open question if the lack of records of *Eoconodon* in smaller samples of Pu1 local faunas in other areas, e.g., Littleton Fauna, Denver Basin, Colorado, or the purported Pu1 faunas of Saskatchewan, is a product of small sample size or absence of the genus from these areas. In either case, the limited distribution of Pu1 occurrences of the genus suggests *Eoconodon* was an immigrant that dispersed into the Western Interior sometime during this interval zone. Presence of what appear to be two distinct Pu1 species of *Eoconodon* raises the question of the timing of their differentiation. Did it occur during the Pu1 interval zone or was it a product of a Cretaceous diversification in some other as yet un-sampled area?

Middle Puercan, Pu2 interval zone.   Pu2 and Pu3 were defined in the San Juan Basin, New Mexico, and they have been clearly identified as far to the north as the Hanna Basin, Wyoming, and, possibly, in Makoshika Park, southeastern Montana.   Attempts to recognize them farther northward and westward have been unsuccessful, probably because of paleobiogeographic provinciality.   Because of the lack of suitable sediments in the San Juan Basin, the durations of the Pu2 and Pu3 interval zones have yet to be determined by radiometric age determinations.   The Pu2 and Pu3 local faunas of this area are preserved in sediments deposited during magnetic polarity chron C29n (Williamson 1996).   The boundaries between chrons C29r and C29n, 65.16 m.y., and C29n and C28r, 64.39 m.y. (Wilson 2005), include an interval of approximately 770,000 years.

In the San Juan Basin, faunas of the Pu2 interval zone are known from large samples obtained primarily by surface collecting and include records of three species of *Eoconodon* – *E. coryphaeus, E. gaudrianus,* and *E. ginibitohia* (Williamson 1996, Clemens and Williamson 2005). Surface collecting in a series of exposures of the North Horn Formation in the Dragon Canyon area, Utah, has yielded a small sample of the Gas Tank local fauna that is tentatively regarded as Pu2 (Lofgren et al. 2005).   *Eoconodon* is not represented in this sample or in the surface collections from the sparsely fossiliferous Corral Bluffs and West Bijou Creek -1 localities in the Denver Basin, Colorado, which could be of either Pu2 or Pu3 age.   A single fragment of an upper molar records the presence of the genus within the Pu2 interval zone in the Hanna Basin, Wyoming, where both surface collecting and screen washing techniques were employed.   More material is needed to determine whether this specimen represents one of the species of *Eoconodon* known from the San Juan Basin, one of the species known from northern Western Interior sites, or a new species.

Late Puercan, Pu3 interval zone.   Faunas that can be definitely assigned a Pu3 age are limited to the San Juan Basin, New Mexico; Dragon Canyon, Utah; and the Hanna Basin, Wyoming.   The local faunas in the San Juan Basin are known from samples obtained by surface collecting.   Two species of *Eoconodon, E. coryphaeus*, and *E. gaudrianus,* are documented but these collections are smaller than those of Pu2 local faunas (Williamson 1996, 2005).   The sample of the Wagonroad fauna was derived by surface collecting of strata of the North Horn Formation exposed in Dragon Canyon, cen-

tral Utah, that record the transition from magnetic polarity chron C29n to C28r.   This fauna was assigned to the Pu3 interval zone by Lofgren et al. (2004).   It has yet to yield a record of *Eoconodon* but includes the type specimen of the "triisodontid" *Goniacodon hiawathae* Van Valen (1978). *Eoconodon* is lacking from the large Pu3 samples in the Hanna Basin.

Undifferentiated Pu2/Pu3 interval zones.   The major collections of this interval are from sites in northeastern Montana, particularly Garfield County, where localities in the Garbani Channel deposits are very productive (Clemens 2002).   Where the magnetostratigraphy has been determined, all of the collecting sites fall within magnetic polarity chron C29n.   Radiometric age determinations obtained in northeastern Montana bracket them in an interval between the boundary between C29r and C29n – 65.16 m.y.– and an age determination of 64.52 ± 0.02 m.y. for a tephra preserved in the W coal, which overlies the Garbani Channel deposits, giving a duration of approximately 640,000 years (Wilson 2005).   The Garbani Channel localities have been worked with a combination of hand quarrying followed by underwater screening.   To date approximately 4,500 mammalian fossils have been cataloged (UCMP online database), but when fully curated the sample of this Pu2/Pu3 fauna probably will be at least three to four times as large.

Both *Eoconodon hutchisoni* and *E. nidhoggi* are represented in the Garbani Channel deposits, and *E. nidhoggi* is typified by a specimen from Purgatory Hill.   Currently *E. hutchisoni* is only known from northeastern Montana.   Isolated teeth from other areas have been tentatively referred to *E. nidhoggi*: *Eoconodon* sp. cf. *E. nidhoggi* from the Simpson Quarry, Bear Formation, south central Montana of Pu2/Pu3 undifferentiated age (Buckley 1994).   A fragmentary lower molar from the Hiatt South locality, Makoshika State Park, southeastern Montana was tentatively referred to *E. nidhoggi* by Hunter et al. (1997) who argued for a Pu2, possibly early Pu2, age assignment.   Finally Johnston and Fox (1984) identified three fragmentary teeth found at Rav W-1, Saskatchewan, as ?*Eoconodon nidhoggi*.   Fox (1997) and Lofgren et al. (2004) tentatively assigned a Pu2 age to this locality.   These occurrences suggest that *E. nidhoggi* ranged over the northern Western Interior during the Pu2 and Pu3 interval zones.   The absence of records of *E. hutchisoni* in areas outside northeastern Montana could well be a product of small collection sizes.

Early Torrejonian, To1 interval zone. As noted above, Standardt (1986, 1995) suggested that *Eoconodon* might be present at a locality in the Tornillo Formation, Texas, which, on the basis of faunal composition, Williamson (1996, p. 66-67) regarded as probably Torrejonian in age. A few isolated teeth from two early Torrejonian local faunas in northeastern Montana, the Farrand Channel and Horsethief Canyon local faunas, document the presence of two "triisodontids" (Clemens and Wilson 2009); one might represent a new species of *Eoconodon*. These records, added to To1 occurrences of species of *Goniacodon* and *Triisodon,* document the increased taxonomic diversity of "triisodontids" in the early Torrejonian.

Summary

Large samples of Lancian local faunas from the northern Western Interior obtained by surface collecting and screen washing techniques lack records of *Eoconodon*, other "triisodontids," or closely related sister groups. Although significantly smaller, samples of Lancian local faunas from the southern Western Interior also lack similar records. Together their absence is in accord with the hypothesis that "triisodontids" or closely related sister groups were not present in the sampled areas of the Western Interior in the latest Cretaceous.

The oldest records of *Eoconodon* are limited to occurrences in two Pu1 local faunas in Wyoming. These specimens document the presence of two species, which indicates some diversification of "triisodontids" during the Cretaceous in areas that have yet to be sampled. *Eoconodon* or other "triisodontids" are absent from the very large samples of Pu1 local faunas and the time-averaged Bug Creek Assemblage localities in the northeastern Montana. Probably *Eoconodon* had not spread throughout the northern Western Interior in the Pu1 interval zone. Contemporaneous local faunas have yet to be discovered in the southern Western Interior.

Large samples of Pu2, Pu3, and Pu2/Pu3 undifferentiated local faunas are available from both the northern and southern Western Interior. During the Pu2 and Pu3 interval zones *Eoconodon* spread its range throughout the Western Interior and differentiated producing distinct groups of northern and southern species. A second genus of "triisodontid," *Goniacodon* made its appearance in the Pu3 Wagonroad local fauna of Utah. The limited available samples of To1 local faunas document the first occurrence of *Triisodon* and suggest further diversification of the species of *Eoconodon.*

CONCLUSIONS

New collections record the presence of two species of *Eoconodon, E. nidhoggi*, and *E. hutchinsoni,* in the Pu2/Pu3 fauna of northeastern Montana. These northern species differ from the three species of *Eoconodon* previously known from the San Juan Basin. Their pattern of distribution supports the hypothesis of biogeographic provinciality in the Western Interior during the Puercan North American Land Mammal Age.

In comparison to the tribosphenic dentitions of primitive eutherians, the dentition of *Eoconodon* and later "triisodontids" is distinctly modified with relatively blunt cusps suggesting emphasis on chopping and crushing functions. By the middle and late Puercan, if not earlier, Hunter-Schreger bands had evolved in the enamel of cheek teeth of *Eoconodon* increasing their resistance to fracturing. Evolution of this derived microstructural pattern could well be associated with increase in body size and adaptations to a more predaceous and/or scavenging mode of feeding.

Particularly in the northern Western Interior, the absence of *Eoconodon* or closely related sister groups from well sampled Lancian faunas suggests that "triisodontids" were not present in this area in the latest Cretaceous. The earliest occurrences of *Eoconodon* are documented in the Mantua local fauna, *E. copanus,* and a second, smaller species in a Pu1 local fauna in the Hanna Basin. This pattern of first occurrences is in line with the hypothesis proposed by Lillegraven and Eberle (1999) and others that many taxa particularly archaic ungulates, first recorded in the Pu1 record of the Western Interior appear to be immigrants. During the Pu2 and Pu3 interval zones the species of *Eoconodon* ranged through the Western Interior and differentiated producing distinct groups of northern and southern species. In the late Puercan (Pu3) a second genus of "triisodontid," *Goniacodon*, appeared in the Western Interior. Samples of early Torrejonian (To1) local faunas are limited but document the first occurrence of *Triisodon* and suggest further diversification of the species of *Eoconodon.*

the majority of our geological and locality data on aerial photographs. The only United States Geological Survey map available covering part of our research area was the Maloney Hill (1958) 15 minute quadrangle. In contrast, 7.5 minute quadrangles covering the valley of Bug Creek and other areas around the Big Dry Arm of Ft. Peck Reservoir were just beginning to be released. I asked Rep when the mapping project would result in topographic maps of the valley of Hell Creek and adjacent areas. He said that he would look into the matter and see what he could do. He did a lot! By 1977, when D. Archibald completed his dissertation research, the preliminary editions of the 7.5 minute Trumbo Ranch and Hell Hollow quadrangles were published and orthophoto quadrangles of adjacent areas were available. In not too many more years we benefited from complete map coverage of our research area. Thanks Rep!

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