

Hemiacodon engardae, a new species of omomyid primate from the earliest Uintan Turtle Bluff Member of the Bridger Formation, southwestern Wyoming, USA

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ABSTRACT

In this paper, we describe a new species of *Hemiacodon* known only from University of Colorado Museum Loc. 92189 (Donna's Locality) in the Turtle Bluff Member of the Bridger Formation, Green River Basin, southwestern Wyoming. Donna's locality has yielded a diverse mostly small-bodied mammalian assemblage of Bridgerian and first appearance Uintan mammalian taxa, as well as range-through taxa. Together with *H. engardae* sp. nov., the faunal assemblage from Donna's Locality and more recently discovered localities in the same stratigraphic interval provides the first conclusive paleontological evidence of an earliest Uintan age (Ui1A biochron) for the Turtle Bluff Member of the Bridger Formation.

The new species is represented by a sample of 11 specimens consisting of well-preserved upper and lower premolars and lower molars. *H. engardae* is distinct from *H. gracilis* on the basis of overall larger size as well as a combination of features of the premolars and molars related to a greater development of shearing crests. This suggests that *H. engardae* may have incorporated more foliage into its diet than the Bridgerian species, *H. gracilis*.

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Introduction

The middle Eocene Bridger Formation of southwestern Wyoming is well known for its abundant and diverse vertebrate fossils. However, the biochronologic age and correlation of the uppermost member of the Bridger Formation has long been uncertain because it is sparsely fossiliferous. Historically, the Turtle Bluff Member (= Bridger E of Matthew, 1909) has been regarded as either Bridgerian or Uintan in age. Matthew (1909: 296) stated that its few fossils prove sufficiently that the Bridger E "belongs to the Bridger age." Without citing any supporting evidence, Osborn (1929) correlated the Bridger E with the early Uintan Washakie B and Uinta B members. Simpson (1933), Wood et al. (1941), and Gazin (1976) also regarded the Bridger E as Uintan, again without presenting evidence. West and Hutchison (1981) concluded that the Bridger E was Bridgerian in age on the basis of scant fossil evidence, including eight isolated rodent teeth identified as *Paramys* cf. *P. delicatior*, a proximal radius identified as belonging to one of the common Bridgerian brontotheres, either *Palaeosyops* or

Manteoceras, and the characteristic Bridgerian turtles *Baptemys wyomingensis* and *Rhinoclemys terrestris*.

While collecting with a University of Colorado Museum (UCM) field party in 1992, Donna Engard discovered a highly fossiliferous locality located stratigraphically two meters above the base of the Turtle Bluff Member (TBM; Figs. 1 and 2). The faunal assemblage of UCM Loc. 92189 (also known as "Donna's Locality") is significant because, as reported by Evanoff et al. (1994), Robinson et al. (2004), Murphey and Evanoff (2007), Murphey and Walsh (2007), and Gunnell et al. (in press), it demonstrates an earliest Uintan age for the TBM, which is in conformable superposition with Bridgerian-age strata of the underlying Twin Buttes Member (= Bridger C and D of Matthew, 1909). Furthermore, the composition of the transitional fauna from Donna's Locality and its close stratigraphic relationship with true Bridgerian faunas of the underlying Bridger D indicate that the locality pre-dates the controversial Shoshonian land mammal "Subage" as presently defined (Flynn, 1986; Murphey and Walsh, 2007; Gunnell et al., in press). The TBM has recently been designated as the stratotype section for the earliest Uintan biochronological zone "Ui1a" as defined by Gunnell et al. (in press).

The faunal assemblage from Donna's Locality consists of 288 specimens of mostly small-bodied taxa including fish, amphibians, reptiles, birds, and mammals. Mammalian fossils include a mix of characteristic Bridgerian taxa along with some Uintan first appearances and range-through taxa. Biostratigraphically

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Figure 1. West-facing exposures of the Bridger Formation located on the southwest flank of Cedar Mountain, Uinta County, Wyoming. Contact between Twin Buttes Member and overlying Turtle Bluff Member occurs at approximate stratigraphic level of lowest red beds.

noteworthy occurrences include the characteristic Uintan rhinocerotoid perissodactyl *Triplopus*, the Uintan eomyid rodent *Metanoimys*, a new genus and species of oromyrid artiodactyl, and a new derived species of the characteristic Bridgerian omomyid primate *Hemiacodon*, which is the subject of this paper. Additional early Uintan taxa that have been subsequently collected from other levels in the TBM include the cylindrodontid rodent *Pareumys*, an unidentified sespedectine insectivore, and a primitive specimen of the equid cf. *Epihippus* (Murphey and Walsh, 2007).

Geologic setting

The Bridger Formation is approximately 842 meters thick and consists of three members. These are, in ascending stratigraphic order, the Blacks Fork, Twin Buttes, and Turtle Bluff. Lithologically, the Blacks Fork and Twin Buttes members are composed of green, brown, and gray mudstone and claystone, scattered ribbon and sheet sandstones, widespread beds of micritic and sparry limestone, and thin but widespread ash fall tuffs. The TBM attains

a maximum thickness of 131 meters on the southwest flank of Cedar Mountain and is composed of predominant variegated red, green, and gray claystone and mudstone with lesser amounts of grayish-white tuffaceous sandstone and gray and brown limestone, and with high gypsum content. Strata of the TBM are unconformably overlain by the Oligocene-age Bishop Conglomerate (Murphey and Evanoff, 2007).

The TBM is stratigraphically equivalent to the Bridger E of Matthew (1909) and the Cedar Mountain Member of West and Hutchison (1981). It was renamed by Evanoff et al. (1998) and described in detail by Murphey and Evanoff (2007). The modern day distribution of the TBM consists of erosional remnants located only in the southern part of the Green River Basin along the northern front of the Uinta Mountains; specifically on Hickey Mountain, Sage Creek Mountain, Cedar Mountain, Twin Buttes, and Black Mountain in Uinta and Sweetwater counties, Wyoming.

UCM Loc. 92189 is stratigraphically situated two meters above the base of the TBM of the Bridger Formation on the southwest flank of Cedar Mountain, Uinta County, Wyoming. A tuffaceous

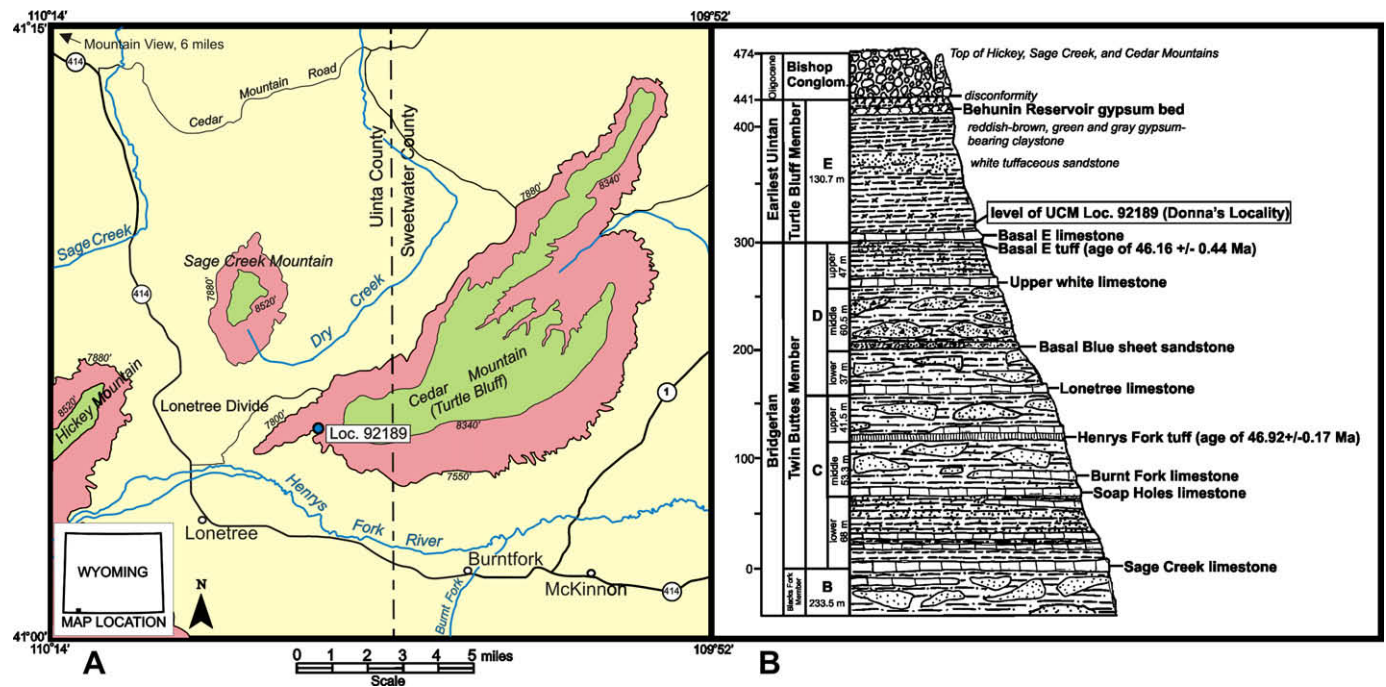


Figure 2. (A) Map of the southern Green River Basin in Wyoming showing the approximate location of UCM Loc. 92189 (Donna's Locality). (B) Generalized stratigraphic section of the upper Bridger Formation (Twin Buttes and Turtle Bluff members) in the vicinity of Hickey Mountain, Sage Creek Mountain, and western Cedar Mountain, Uinta County, Wyoming (adapted from Murphey and Evanoff, 2007).

pumiceous sandstone bed (named “Basal E tuff” by Murphey and Evanoff [2007]) is situated eight meters below the base of the TBM on nearby Sage Creek Mountain. This unit was found to have an isotopic age 46.16 ± 0.44 Ma using $^{40}\text{Ar}/^{39}\text{Ar}$ analysis (Murphey et al., 1999; Murphey and Evanoff, 2007; see Murphey and Evanoff [2007] for additional lithostratigraphic details). Therefore the faunal assemblage from UCM Loc. 92189 has an age of approximately 46 Ma. Based on the age of the Basal E tuff as reported by Murphey and Evanoff (2007), it is likely that the entire TBM is correlative with part of chron C20r as calibrated by Berggren et al. (1995).

Description of *Hemiacodon engardae*

Abbreviations: CM = Carnegie Museum of Natural History; UCM = University of Colorado Museum of Natural History.

Systematic paleontology

Order PRIMATES Linnaeus, 1758
 Infraorder TARSIFORMES Gregory, 1915
 Family OMOMYIDAE Trouessart, 1879
 Subfamily OMOMYINAE Trouessart, 1879
 Genus HEMACODON Marsh, 1872
***Hemiacodon engardae* sp. nov.**
 (Figs. 3 and 4)

Holotype

UCM 67874, right dentary fragment with P₃-M₂.

Known distribution

Locality UCM Loc. 92189 (biochron Ui1A).

Etymology

In honor of the late Donna Engard, the first Curator of the Dinosaur Depot Museum in Cañon City, Colorado, and an avid fossil hunter who discovered Loc. 92189.

Hypodigm

The type specimen and UCM 67785 (right dentary fragment with RM₂₋₃), UCM 68907 (isolated RM₃), UCM 68426 (isolated right trigonid), UCM 68920 (fragmentary LP⁴), UCM 70086 (isolated RM₃), UCM 70087 (worn isolated RM₂), UCM 70089 (isolated RM₁), UCM 70090 (LP₃), UCM 95689 (RP³), and UCM 70672 (dentary fragment with RP₃₋₄).

Specific diagnosis

Differs from *Hemiacodon gracilis* in having P³ with straight rather than flexed mesial border; larger P³ metacone; P⁴ with larger metastyle and metacone; P₃ with small paraconid (as opposed to none); P₄ paraconid larger and situated along lingual margin of tooth rather than in line with the protoconid; well developed lingually positioned metaconid on P₄; molar trigonids with well developed crests extending mesially and distally from the paraconid and metaconid; longer molar postmetacristid and entocristid; narrower molar talonid notch; M₁₋₂ paracristids that are straight and meet the paraconid at a sharp angle mesially, rather than being less distinct, curved, and joining the paraconid more buccally; M₁ protocristid that does not reach the metaconid; M₂ with crest-like, lingually positioned paraconid that is less reduced;

M₂ metaconid crest-like and aligned with paraconid. Differs from *Hemiacodon casamissus* in larger molar size and in having a P₃ postvallid that is transversely oriented to the long axis of the tooth (rather than obliquely oriented).

Dental description

The occlusal surface of P³ consists of a single main cusp, the metacone, which is high and transversely wide. The lingual aspect of the tooth is reduced with respect to the buccal margin and the protocone is small and situated near the mesial aspect of the tooth. The mesial margin is straight, and there is a continuous cingulum on all sides of the tooth. The P⁴ consists only of the buccal half of the tooth. The metacone and metastyle are well developed, and the paracone is small but distinct. The metacone is situated on the buccal margin of the tooth and connected to the metastyle by a crest that curves buccally.

The oblique orientation of the P₃ in the holotype is due to post-mortem avulsion of the tooth from the alveolus. The P₃ is dominated by the protoconid and lacks a metaconid, but a small paraconid is evident on the mesio-lingual aspect of the tooth. The paracristid descends the mesial aspect of the protoconid and joins the base of the paraconid. The postvallid faces distally and is bounded buccally and lingually by two crests, making it appear concave. The P₄ has a fully-developed trigonid with subequal proto-, para-, and metaconids. The para- and protoconids are joined by a sharp, straight paracristid. The protocristid extends lingually from the protoconid towards the metaconid to contact the metaconid at its base. The para- and metaconids are not joined, resulting in a lingually open trigonid. The postvallid of the P₄ is bounded by two crests, much like that of the P₃, except that the lingual crest on the P₄ is not as well developed as that on the P₃.

The M₁ of *Hemiacodon engardae* is characterized by elongated shearing crests and extremely crenulated enamel. The hypoconid is buccally positioned, giving the tooth a distinctly wider talonid than trigonid, as is characteristic of the other species of *Hemiacodon*. The cristid obliqua is straight and joins the postvallid just buccal to the midline. The hypoconulid is distinct and located directly distally on the edge of the talonid, and the buccal cingulid is strong. The trigonid of M₁ is triangular in occlusal view due to the straight, strong protocristid that joins the paraconid on its mesial edge, and to the lingual position of the paraconid. In lingual view, strong crests that extend from the mesial and distal aspects of the paraconid and metaconid contribute to a blade-like lingual surface of the trigonid. The postmetacristid is similarly expanded in lingual view. A strong fold of enamel originates on the buccal margin of the metaconid cusp and extends into the talonid basin. As a consequence, the protocristid does not join the metaconid but stops abruptly against the buccal edge of the metaconid.

The M₂ of *Hemiacodon engardae* generally resembles the M₁ but with some modifications. The paraconid is more buccally shifted compared to M₁ and is less cusped. In lingual view, the paraconid and metaconid are united for most of their height whereas in M₁ they are separate.

The hypoconulid lobe of M₃ is greatly expanded, making the tooth much longer than M₁ or M₂, but overall this molar resembles the other two. The paraconid and metaconid are united and blade-like as in M₂, but the paraconid is reduced and more buccally situated. The metaconid is reduced and often indistinct or made up of multiple small cusps, giving the trigonid a rugose appearance.

Comparisons

In addition to this new species, two other species of *Hemiacodon* have been previously described. *H. gracilis*, the type species of the

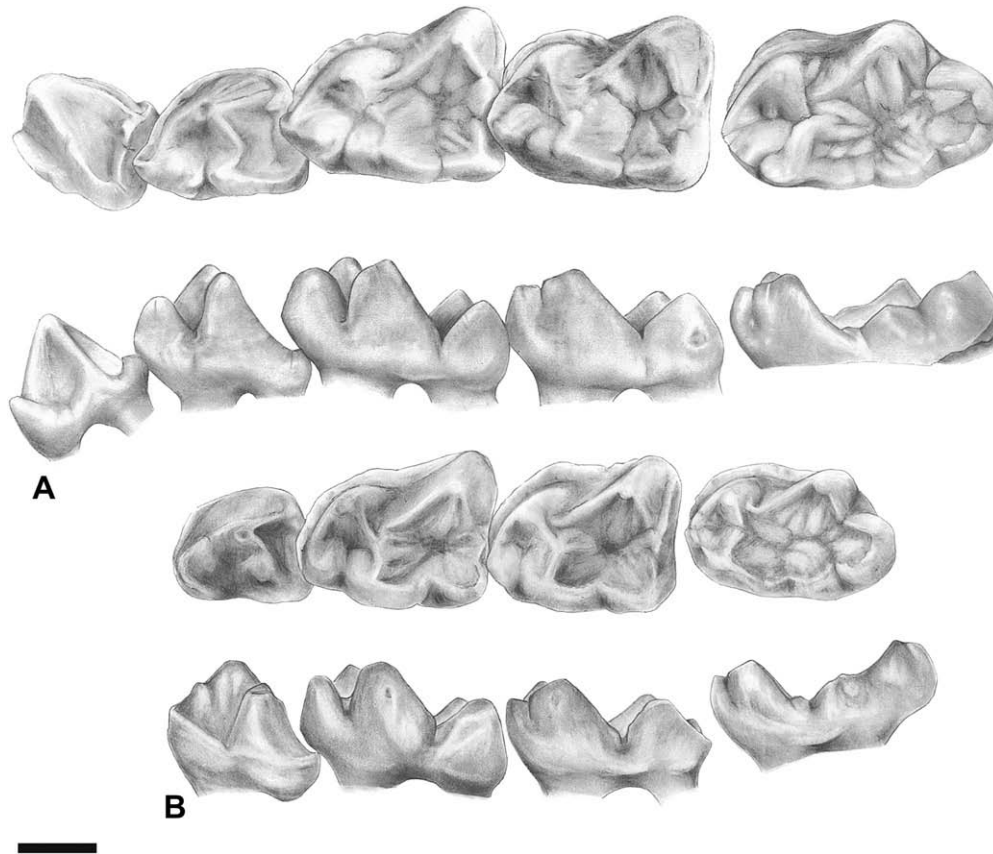


Figure 3. Dentition of *Hemicodon engardae* compared to *H. gracilis* from the Bridger D. (A) *H. engardae* (UCM 67874, right P₃-M₂, holotype and UCM 68907, right M₃) in occlusal view (top) and lingual view (bottom). (B) *H. gracilis* (UCM 70051, right P₄-M₃) in occlusal view (top) and lingual view (bottom). Scale = 2 mm.

genus, is most abundant in biochronological zone Br3 (Bridger C-D of Matthew, 1909) but is also known from zone Br2 (= Bridger B of Matthew, 1909). This taxon is represented by a large number of well-preserved and complete dental specimens, making it one of the best known Eocene primates (Szalay, 1976; Gunnell and Rose, 2002). *H. casamissus* (Beard et al., 1992) is a somewhat enigmatic taxon represented by one specimen (CM 62035) from the latest Wasatchian (Lostcabinian, biochronological zone Wa7) of the Wind River Formation. CM 62035 consists of a right dentary fragment with worn M₁₋₂ and an isolated unworn P₃. As discussed by Gunnell (1995: 179–180), the association of the P₃ with the M₁₋₂ which comprises this specimen is questionable due to differential wear, making its relevance for discussing the relationships of *Hemicodon* problematic. Comparisons are made primarily with *H. gracilis* and with *H. casamissus* when possible.

The P₃ of *H. engardae* differs in occlusal outline from that of *H. gracilis* in having a mesial margin that is straight bucco-lingually rather than flexed inwards, giving this tooth a more waisted appearance in *H. gracilis*. In addition, the buccal margin of the P₃ in *H. engardae* appears to be mesiodistally longer and the metacone slightly larger than in *H. gracilis*. The P₄ of *H. engardae* differs from that of *H. gracilis* in the greater development of the metastyle and metacone and in the more buccal placement of the metacone. In *H. gracilis*, the metacone is more lingually situated and joined to the metastyle by a straight crest.

The P₃ of *Hemicodon engardae* and *H. gracilis* are similar overall, although *H. engardae* is slightly more “cresty” in appearance. The postvallid resembles that of *H. gracilis* in being transversely oriented to the long axis of the tooth rather than that of *H. casamissus* in which it is obliquely oriented. The P₄ of *H. engardae* is

more molariform than that of *H. gracilis* with a well-developed, lingually positioned paraconid and a better developed metaconid, whereas the P₄ of *H. gracilis* has a poorly-developed, more buccally shifted paraconid and a smaller metaconid. Buccal and lingual postvallid crests are generally absent to weak in *H. gracilis*, although there is a significant amount of variation. While the Bridger C specimens examined lack a P₄ paraconid, some Bridger D specimens exhibit an intermediate condition with the development of a small mesial paraconid cusp located on the paracristid.

The lower molars of both *H. engardae* and *H. gracilis* exhibit variable crenulation. On average, the lower molars of *H. engardae* are larger than those of *H. gracilis*, although the molar size ranges of the two species overlap (Table 1, Fig. 5). The lower molar crests of *H. engardae* are in general higher and sharper than those of *H. gracilis*. The greatest differences in the lower molars are exhibited in the details of the trigonid morphology. The paracristid of *H. engardae* is comparatively straight and forms a distinct crest that is oblique to the long axis of the tooth, while the paracristid of *H. gracilis* forms a poorly developed crest that is more curved mesially. In addition, the paraconid of *H. gracilis* is located more buccally compared to that of *H. engardae*. The combination of these two features give the M₁₋₂ trigonids of *H. engardae* a distinctly more triangular outline in occlusal view than that of *H. gracilis*, which is more rounded mesially. The lingual trigonid crests of *H. engardae* are relatively more expanded than those of *H. gracilis* and the lingual surfaces of the trigonids are consequently more blade-like. In *H. gracilis* the protocristid is only sometimes broken on M₁₋₂, whereas the protocristid of *H. engardae* is usually broken due to the distinct fold of enamel on the postvallid. The M₂ paraconid of *H. gracilis* is significantly reduced in relation to that of M₁ and

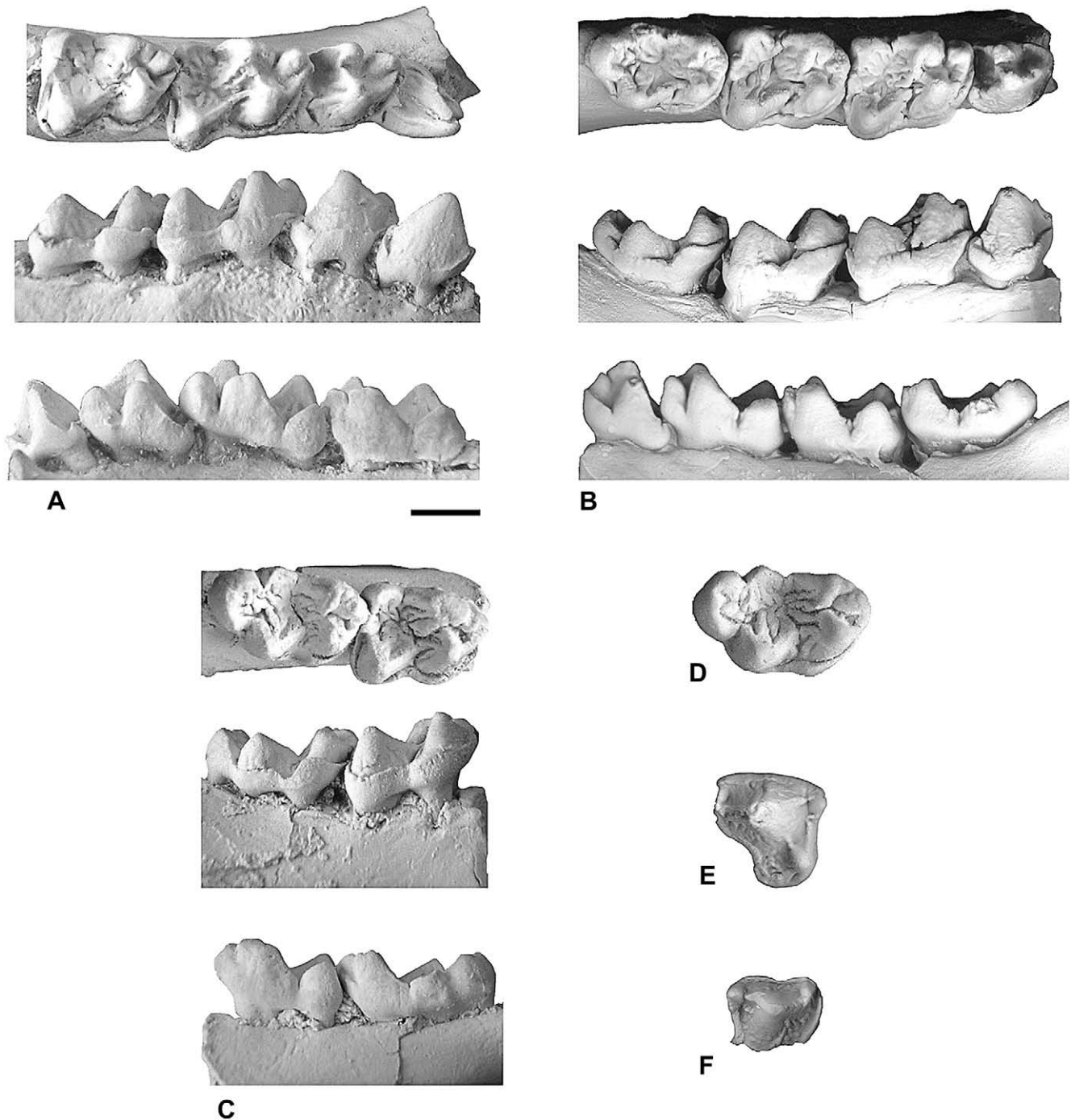


Figure 4. Dentition of *Hemicodon engardae* compared to *H. gracilis* from the Bridger D. (A) *H. engardae* (UCM 67874, right P₃-M₂, holotype) in occlusal view (top), buccal view (middle), and lingual view (bottom). (B) *H. gracilis* (UCM 70051, right P₄-M₃) in occlusal view (top), buccal view (middle), and lingual view (bottom). (C) *H. engardae* (UCM 67785, right M₂₋₃) in occlusal view (top), buccal view (middle), and lingual view (bottom). (D) *H. engardae* (UCM 68907, right M₃) in occlusal view. (E) *H. engardae* (UCM 95689, right P³) in occlusal view. (F) *H. engardae* (UCM 68920, left P⁴) in occlusal view. Note the better developed P₄ paraconid and well developed P₄ trigonid, more triangular molar trigonids, longer and straighter M₁₋₂ paracristid, more lingually placed paraconid on M₁₋₂, more lingually expanded M₁₋₂ trigonid relative to talonid, narrower talonid notch, and overall larger size of *H. engardae* compared to *H. gracilis*. Scale = 2 mm.

positioned mesially, while that of *H. engardae* is only slightly smaller than the corresponding cusp on M₁ and is more lingually positioned. The paraconid and metaconid of *H. engardae* are distinctly less bulbous and more crest-like than *H. gracilis*, in which the paraconid and metaconid are distinct bulbous cusps and are not aligned with each other.

The morphology of the molar talonid basins of *Hemicodon engardae* generally resembles that of *H. gracilis*, but there are some

subtle differences. The postmetacristid of *H. engardae* is distally elongated and well developed in comparison to that of *H. gracilis* which, when viewed lingually, gives the appearance that the trigonid being about twice the length of the talonid. In *H. gracilis*, the lingual margin of the tooth is more equally divided between the trigonid and talonid. The talonid notch on all lower molars of *H. engardae* is reduced when viewed from the lingual aspect in comparison to that of *H. gracilis* due to the expansion of the

Table 1
Dental measurements (in mm) of specimens of *Hemicodon gracilis* and *H. engardae* in the UCM collections, and the holotype and only known specimen of *H. casamissus* (CM 62035).

	P ₃ length	P ₃ width	P ₄ length	P ₄ width	M ₁ length	M ₁ trigonid width	M ₁ talonid width	M ₂ length	M ₂ trigonid width	M ₂ talonid width	M ₃ length	M ₃ trigonid width	M ₃ talonid width
<i>H. casamissus</i>	2.75	1.85	–	–	2.9	–	2.35	3.2	–	2.6	–	–	–
<i>H. gracilis</i>													
n	3	3	5	5	16	17	17	24	24	24	13	14	14
Mean	2.96	2.07	2.89	3.13	3.69	2.70	2.92	3.52	2.87	2.97	4.02	2.53	2.35
Min	2.86	1.95	2.61	1.91	3.12	2.46	2.75	3.08	2.60	2.67	3.49	2.24	2.27
Max	3.09	2.14	3.08	2.30	4.00	2.96	3.17	4.11	3.19	3.28	4.81	2.71	2.78
<i>H. engardae</i>													
n	3	3	2	2	1	1	1	4	4	4	3	3	3
Mean	2.84	2.19	3.11	2.44	3.84	2.88	3.01	3.88	2.81	3.04	4.55	2.73	2.76
Min	2.62	2.12	2.92	2.37	–	–	–	3.77	2.50	2.91	4.24	2.66	2.73
Max	3.07	2.22	3.29	2.51	–	–	–	3.94	2.97	3.10	4.71	2.78	2.81

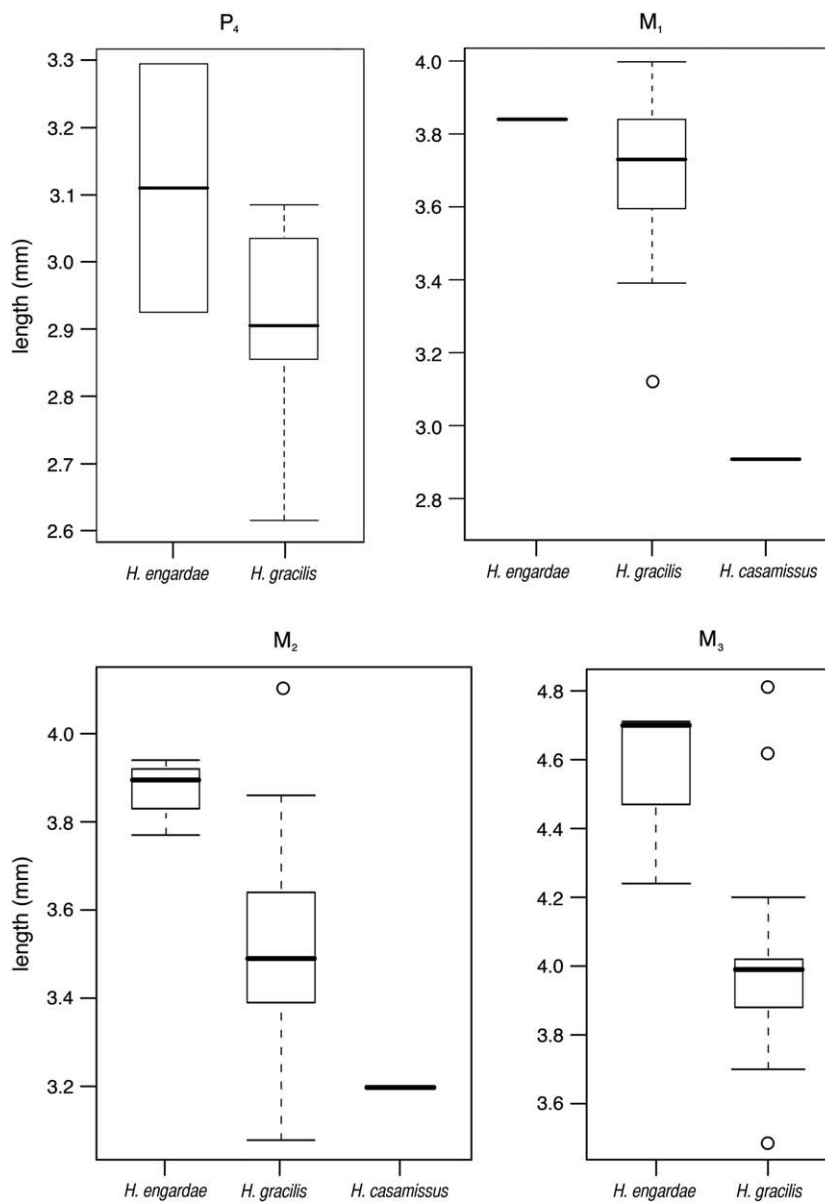


Figure 5. Boxplots of P₄, M₁, M₂, and M₃ length in specimens of *Hemicodon engardae* and *H. gracilis* from the UCM collections and the holotype of *H. casamissus* (CM 62035). Note that the teeth of *H. engardae* are larger on average than those of the other species of *Hemicodon*, but that there is a large amount of variation in the size of *H. gracilis*. Heavy bar indicates the median, box encompasses the central 50% of the distribution, whiskers encompass central 75% of the distribution, and circles are outliers. Measurements listed in Table 1.

postmetacristid and entocristid. This is in contrast to the wide talonid notch seen in *H. casamissus*. The hypoconulid lobe on M₃ of *H. engardae* is larger on average than that of *H. gracilis*.

Discussion

Hemicacodon gracilis is generally regarded to have been folivorous based upon its relatively large body size, broad molar talonids, well-developed cingula, crenulated enamel, and well-developed shearing crests (Szalay, 1976; Gunnell and Rose, 2002; Gilbert, 2005). The larger size of *H. engardae* compared to *H. gracilis* in combination with the increased emphasis on shearing crests of the lower molars and P₄ suggests that *H. engardae* was incorporating more foliage into its diet than *H. gracilis* (Kay, 1984). These features have also been noted in *Macrotarsius* (Szalay, 1976; Gunnell and Rose, 2002) and may support a close relationship between the two genera, although a rigorous phylogenetic analysis is needed to address this question.

There is considerable uncertainty surrounding the phylogenetic position of *Hemicacodon* despite the fact that it is well known both dentally (Szalay, 1976; Gunnell, 1995) and postcranially (Simpson, 1940). Two major hypotheses have emerged. The first states that *Hemicacodon* is a derived member of the Washakiini, a clade consisting of *Washakius*, *Shoshonius*, *Loveina*, and *Dyseolemur* (Szalay, 1976; Krishtalka and Schwartz, 1978; Beard et al., 1992). The second places *Hemicacodon* as the sister taxon to the Omomyini which includes *Omomys*, *Chumashius*, *Ourayia*, and *Macrotarsius* (Honey, 1990). Gunnell (1995) united *Hemicacodon* and *Macrotarsius* in a tribe (Macrotarsiini) as the sister taxon to an *Omomys/Chumashius* clade, noting that this hypothesis is a variant of that put forth by Honey (1990). Gunnell and Rose (2002) suggest a washakiini ancestry for macrotarsiins, which is more consistent with the first hypothesis. The phylogenetic uncertainty stems in large part from the extremely derived lower molar morphology of *Hemicacodon gracilis* (Gazin, 1958; Szalay, 1976; Honey, 1990; Beard et al., 1992; Gunnell, 1995; Gunnell and Rose, 2002). Recent cladistic analyses of omomyoid relationships have supported some variation of Honey's (1990) hypothesis in placing *Hemicacodon* as a basal member of an omomyin-like clade and outside of the Washakiini (Williams, 1994; Tornow, 2005, 2008). The incorporation of *H. engardae* into future analyses of omomyoid phylogeny hopefully will contribute to the resolution of this issue.

As currently understood, the middle Eocene North American Land Mammal "Ages" consist of the Bridgerian, the Uintan, and the Duchesnean, from oldest to youngest (see Robinson et al., 2004). The Uintan was an important time period during which selenodont artiodactyls evolved and radiated, and there were family-level diversifications of rodents and rhinocerotoid perissodactyls. The transition from Bridgerian to Uintan faunas is generally associated with a decline in diversity of certain archaic mammalian groups such as uintatheres, North American primates, hypsodontid condylarths, and oxyaenid creodonts (Rasmussen et al., 1999; Woodburne, 2004). Because few continuous fossiliferous sequences across this interval are known, and all are sparsely fossiliferous or poorly sampled, the Bridgerian-Uintan transition is particularly difficult to investigate and represents one of the most problematic issues of Eocene biochronology. *Hemicacodon engardae*, in combination with the assemblage of Bridgerian and first appearance Uintan mammalian taxa discovered at UCM Loc. 92189 (Evanoff et al., 1994) and at more recently discovered localities (Gunnell et al., in press; Murphey and Walsh, 2007) in the TBM, provides paleontological evidence that is critical to an understanding of the nature and timing of the Bridgerian-Uintan faunal transition and at long last permits a characterization of the earliest Uintan mammalian fauna.

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