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ABSTRACT—*Castor*, the extant beaver, is an important member of North American and Eurasian communities, altering ecosystems and landscapes wherever it occurs. *Castor* has a fossil record extending back to the late Miocene in Europe, Asia, and North America. The origin and early evolution of this genus is unclear but it likely originated in Eurasia and subsequently dispersed to North America from Asia in the late Miocene. A new record of *Castor* from the Rattlesnake Formation of Oregon represents the earliest occurrence of the genus in North America. The age of this new find is inferred through radiometric and magnetostratigraphic dating to be between 7.05 and 7.3 Ma. This age is supported by the co-occurrence of another beaver, *Dipoides stirtoni*, which is characteristic of early Hemphillian deposits. This find indicates that *Castor* had dispersed to North America by the early Hemphillian, and helps resolve the timing of divergence between North American and Eurasian beavers. The Rattlesnake Formation specimens are not differentiable from other North American specimens of *C. californicus* in morphology or size. This suggests *Castor* changed little after dispersing to North America, whereas the endemic castoroidine beavers changed dramatically after its arrival.

INTRODUCTION

THE EXTANT beaver, *Castor*, is represented by two species: the North American *C. canadensis* (Kuhl, 1820) and the Eurasian *C. fiber* (Linnaeus, 1758). Prior to human exploitation, *Castor* had a Holarctic distribution and was incredibly abundant (Müller-Schwarze and Sun, 2003). Beavers are well known for their semi-aquatic habits and their tree-cutting and dam-building behaviors. Both living species are considered ecosystem engineers, heavily modifying forest and waterway ecosystems throughout their range (Naiman et al., 1988; Butler, 1995; Wright and Jones, 2002; Müller-Schwarze and Sun, 2003; Rosell et al., 2005).

Although the two extant *Castor* species are all that remains, the fossil history of beavers includes approximately 30 genera. Beavers first appeared in the late Eocene of North America and subsequently dispersed to Eurasia (Korth, 1994; Flynn and Jacobs, 2008). The family shows a general trend of increasing hypsodonty over the Tertiary (Stirton, 1935, 1947) and underwent several adaptive radiations, including fossorial and semi-aquatic lineages (Martin and Bennett, 1977; Martin, 1987; Korth, 1994; Hugueney and Escuillié, 1996; Korth and Rybczynski, 2003; Rybczynski, 2007; Samuels and Van Valkenburgh, 2008; Samuels and Van Valkenburgh, 2009). Biogeographic evidence suggests beavers dispersed across the Bering land bridge multiple times over the Tertiary (Hugueney and Escuillié, 1996; Rybczynski, 2007; Flynn and Jacobs, 2008).

The semi-aquatic lineage that eventually gave rise to *Castor*, the Castorinae, first appeared in the Oligocene of Europe (Hugueney, 1999). The site of origin and dispersal of the genus *Castor* is still a mystery, as it is known from the late Miocene of Europe, Asia, and North America (Stirton, 1935; Xu, 1994; McKenna and Bell, 1997; Hugueney, 1999; Rybczynski, 2007; Flynn and Jacobs, 2008; Rybczynski et al., 2010). The oldest known record of *Castor* may be the rare *C. neglectus* (Schlosser, 1902) from the late Miocene of Germany, approximately 10–12 Ma (MN9) (Hugueney, 1999).

Castor likely immigrated to North America from Asia in the late Miocene (Flynn and Jacobs, 2008). Early records of *Castor* in North America include specimens of *C. californicus* from a number of Hemphillian sites in California, Oregon, and

Nebraska. The type of *C. californicus* (Kellogg, 1911) was described from the North Dome of the Kettleman Hills, upper Etchegoin Formation in Fresno County California (Kellogg, 1911; Stirton, 1935). The Etchegoin Formation spans from the late early Hemphillian to the early Blancan in age (Hosford Scheirer and Magoon, 2007; Janis et al., 2008), between 7.0 +/− 1.2 Ma for the lower portion (Obradovich et al., 1978) and 4.1 +/− 0.2 Ma for the uppermost (Sarna-Wojcicki et al., 1991), but the type and paratypes of *C. californicus* come from the upper part of the section.

Early occurrences of *Castor* from the Hemphillian of Oregon include the Rome Formation of southeastern Oregon (Wilson, 1937) and the Shutler Formation (McKay Reservoir, Arlington, and Ordnance localities) in Northern Oregon (Martin, 2008). Radiometric dates are not available for these sites, but biostratigraphic correlations have been used to infer a late early Hemphillian age for the Rome Formation and late Hemphillian age for the Shutler Formation localities (Tedford et al., 2004; Martin, 2008).

Several early records of *Castor* are known from Nebraska within the Snake Creek and Ash Hollow Formations (Flynn and Jacobs, 2008). The earliest of these records may be the "pits of *Pliohippus* Draw" from the *Aphelops* Draw Fauna of the Johnson Member, Snake Creek Formation, which dates to the late early Hemphillian (Matthew, 1932; Skinner et al., 1977). *C. californicus* is also known from the late Hemphillian aged Mailbox, Devil's Nest Airstrip, and Santee Local Faunas, in the Ash Hollow Formation (Voorhies, 1990). Radiometric dates are not available for most of the Nebraska occurrences but one radiometric date indicates the Santee Local Fauna has an upper age of 5.0 +/− 0.2 Ma (Voorhies, 1990; Boellstorff, 1978).

Castor fossils are widespread and abundant throughout the Plio-Pleistocene of North America. Some of the best *Castor* material in North America comes from the Pliocene aged Glenns Ferry Formation of Idaho. Specimens from the Glenns Ferry Formation were originally described as two species but were synonymized by Conrad (1980) and Repenning et al., (1995). *Castor californicus* is one of the most abundant organisms in the Hagerman Local Fauna (Zakrzewski, 1969;

Ruez, 2009) and is represented by large samples and multiple nearly complete skeletons, providing excellent material for comparisons.

The teeth of *Castor* described in this paper, from the late early Hemphillian aged Rattlesnake Formation of Oregon, represent the earliest well-dated occurrence of the genus in North America and place a minimum date on its dispersal to this continent. Given the importance of beavers in modern ecosystems, understanding the evolution and biogeography of *Castor* is particularly important.

METHODS

Tooth measurements were made with Mitutoyo Absolute digital calipers to the nearest 0.01 mm. Measurements were taken at the occlusal surface of the cheek teeth and included anteroposterior length and transverse breadth. Comparisons were made with known specimens of *Castor californicus* from the National Museum of Natural History, Hagerman Fossil Beds National Monument, and the Idaho Museum of Natural History, as well as photographs and measurements in several publications (including Wilson, 1933; Stirton, 1935; Shotwell, 1970; Gustafson, 1978; Van Tassell et al., 2007; Martin, 2008). Dental nomenclature used in comparative descriptions follows Stirton (1935).

Specimen repositories.—JODA, John Day Fossil Beds National Monument, Kimberly, Oregon; HAFO, Hagerman Fossil Beds National Monument, Hagerman, Idaho; USNM, United States National Museum of Natural History; IMNH, Idaho Museum of Natural History; UOMNH, University of Oregon Museum of Natural and Cultural History, Condon Fossil Collection.

GEOLOGICAL SETTING

The John Day Basin in eastern Oregon include hundreds of fossil localities from the Eocene through the Pliocene epochs, many of these are protected within John Day Fossil Beds National Monument (JODA) and neighboring Bureau of Land Management lands. The uppermost unit exposed in the Picture Gorge area is the late Miocene Rattlesnake Formation. The area west of Dayville, Oregon was first examined by Merriam (1901) and established as the type area of the Rattlesnake Formation by Merriam et al. (1925) and later studied by Enlows (1976) (Fig. 1). The Rattlesnake Formation was chosen as a reference fauna for the Hemphillian Land Mammal Age when it was originally designated (Wood et al., 1941). Studies confirm a Hemphillian age for the faunas (Martin, 1983, 1996; Fremd et al., 1994; Tedford et al., 2004), an assignment with which the authors agree.

The geology in the study area consists primarily of fluvial deposits, including conglomerates, siltstones, and sandstones (Enlows, 1976; Martin, 1996; Martin and Fremd, 2001). The specimens were found as surface float on top of a gently sloping northeast trending ridge, which is covered in many small exposures of reddish brown siltstone. Isolated exposures in the Rattlesnake Formation generally have little exposed stratigraphy, making correlation of their exact position within a stratigraphic section difficult. The Rattlesnake Formation includes a very prominent volcanic ash layer, the Rattlesnake Ash Flow Tuff (RAFT), which has been $^{40}Ar/^{39}Ar$ dated to 7.05 +/− 0.01 Ma (Streck and Grunder, 1995). While the RAFT is not exposed in the study area itself, regional correlation confirms this site lies well below the RAFT. The specimens also lie above an undated white vitric tuff ("Ted's Tuff"), which forms a marker bed within the lower Rattlesnake Formation about 16.5 m above the base of the section (Retallack, 1999; Retallack et al., 2002). Paleomagnetic stratigraphy has been
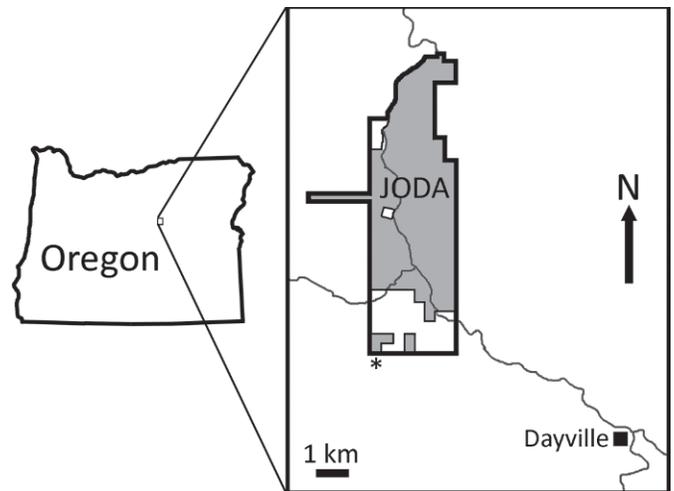

FIGURE 1—Map showing the area where the specimens described here were found (indicated by an asterisk), in the vicinity of the Sheep Rock unit of John Day Fossil Beds National Monument, Grant County, Oregon. JODA=John Day Fossil Beds National Monument.

used to correlate the type Rattlesnake section with magnetic Chrons C3Bn to C3Br2n (6.9–7.3 Ma), confirming a late early Hemphillian age for the entire formation (Prothero et al., 2006). The Rattlesnake Formation unconformably overlies the Barstovian (middle Miocene) aged Mascall Formation.

In his discussion of Merriam's type area, Enlows (1976) described three members of the Rattlesnake Formation, including a lower fanglomerate member, the Rattlesnake Ash Flow Tuff (called Rattlesnake Ignimbrite), and an upper fanglomerate member. These fanglomerate members, and the important faunas from them, were effectively orphaned when Walker (1979, 1990) redefined the Rattlesnake Formation as only including the Rattlesnake Ash Flow Tuff. Martin (1996) suggested regarding the Rattlesnake Formation as being comprised of three members, while Martin and Fremd (2001) proposed elevating it to group status, with three formation-rank units. Revision of these units is outside the scope of this paper, but a formal revision and delineation of these strata is in progress by Martin and Fremd (Fremd, personal comm.). Here, we will use the broader definition of Rattlesnake Formation, as in a variety of other studies (e.g., Retallack et al., 2002; Prothero et al., 2006).

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758
Order RODENTIA Bowditch, 1821
Family CASTORIDAE Hemprich, 1820
Genus CASTOR Linnaeus, 1758
CASTOR CALIFORNICUS Kellogg, 1911
Figure 2

Material.—JODA 13984 (Fig. 2.1 and Fig. 2.2): left m1 and m2. Specimens were found in close proximity (centimeters apart) and collected by J. Zancanella on 19 February 2010; additional materials, including fragments of these teeth, were collected on 15 April 2010 by J. Samuels.

Locality.—lower fanglomerate member of the Rattlesnake Formation, west of Dayville, Grant County, Oregon; approximately 792 m above mean sea level. This area lies within the type area of Merriam, on land administered by the Bureau of Land Management just south of the Sheep Rock Unit of John Day Fossil Beds National Monument (Fig. 1). Precise locality information, including GPS data, is on file at JODA.
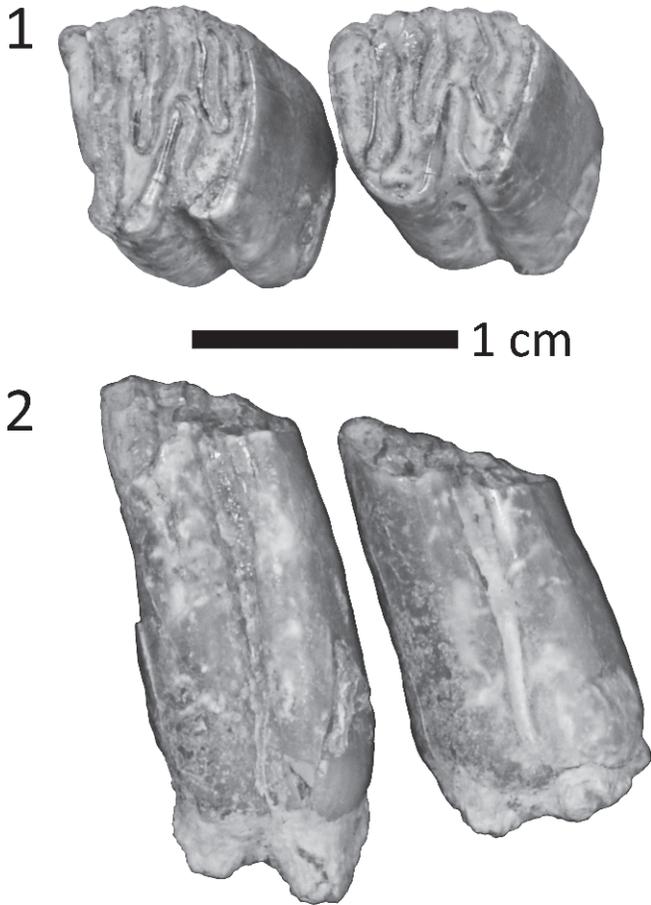
FIGURE 2—Left m1 and m2 of *Castor californicus* (Kellogg, 1911) from the late early Hemphillian-aged Rattlesnake Formation, Oregon: *1*, JODA 13984 occlusal view; *2*, labial view.

Description.—The two specimens consist of a left m1 (JODA 13984*a*) and left m2 (JODA 13984*b*), that, given their close proximity and similar preservation, likely belonged to a single individual. Diagnostic of *Castor*, the cheek teeth are hypsodont with one external and three internal striids on the lower cheek teeth. Both specimens are hypsodont and appear to be from an old individual, indicated by the presence of small well-formed roots on each tooth, as well as their lack of curvature. All flexids display rounded ends. The hypostriids on both specimens extend to the base of the enamel. As is characteristic of *Castor californicus*, the internal striids are unequal in length, with the parastriid being the longest of these, and unlike modern species none of the internal striids reach the base of the enamel.

The m1, JODA 13984a, has some damage to the upper anterior portion of the tooth, with a small portion of the enamel missing. The paraflexid is straight and crosses more than 80% of the occlusal surface. The mesoflexid trends anteriorly and crosses more than half of the occlusal surface. The hypoflexid trends posteriorly, crosses more than half of the occlusal surface, and ends opposite the metaflexid. The metaflexid crosses about half of the occlusal surface and directed posteriorly where it abuts the hypoflexid.

The m2, JODA 13984b, has some damage to the lingual surface of the tooth. The paraflexid is curved slightly anteriorly and crosses more than 80% of the occlusal surface. As in the m1, the mesoflexid trends anteriorly and crosses more than half of the occlusal surface. The hypoflexid trends posteriorly, crosses more than half of the occlusal surface, and ends opposite the metaflexid. The metaflexid crosses more than half of the occlusal surface and has a pronounced zig-zag shape.

DISCUSSION

Though only represented by a pair of teeth, the specimens from the Rattlesnake Formation are not differentiable from known specimens of *Castor californicus*. The characteristics observed in the two specimens from the lower Rattlesnake Formation fall within the range of morphological variation observed in *C. californicus*. These specimens appear similar to other specimens from the Hemphillian of Oregon (McKay Reservoir and Ordanance Faunas; Martin, 2008) and the Blancan of Idaho (Hagerman Local Fauna). Measurements of the Rattlesnake specimens fall within the range of measurements taken from Hagerman specimens (Table 1, Appendix 1). As in extant and extinct *Castor*, the hypostriids extend to the base of the enamel on the teeth from the Rattlesnake Formation. As in *Castor californicus* from Hagerman, none of the three internal striids reach the base of the enamel.

The teeth of *Castor* are known for their intraspecific variability, and change dramatically in morphology and size through wear (Lönnberg, 1909; Hünermann, 1966; Stefen, 2009). Stefen (2009) found the teeth of juvenile to old individuals to show as much as 30% variation in size. Additionally, the pattern of enamel folds and islands of the cheek teeth depend on both age and individual wear. Taken together, evidence of intraspecific variability of castorid teeth should encourage caution in using small samples or differences to differentiate between fossil beaver species.

Specimens of *Dipoides stirtoni* (Wilson, 1934), including a left p 4, left m1 or m2, and right M1 or M2 (JODA 14098, Fig. 3) were found less than a meter from the *Castor* teeth described here; this species is commonly found in the Rattlesnake Formation. The proximity and similar preservation of these *Dipoides* teeth support the contention that these *Castor* specimens truly originate from late early Hemphillian age strata, rather than some later Pliocene or Pleistocene alluvial deposit. The presence of these two beaver species, along with specimens of an emydid pond turtle, suggests an aquatic environment is represented at this locality.

This find represents the earliest known and dated occurrence of *Castor* in North America. The position of this locality within the Rattlesnake Formation, relative to a dated ash bed

TABLE *1*—Measurements (in mm) of *Castor californicus* teeth from Oregon and Idaho; AP=anteroposterior length, T=transverse breadth; measurements for individual specimens are included in Appendix 1.

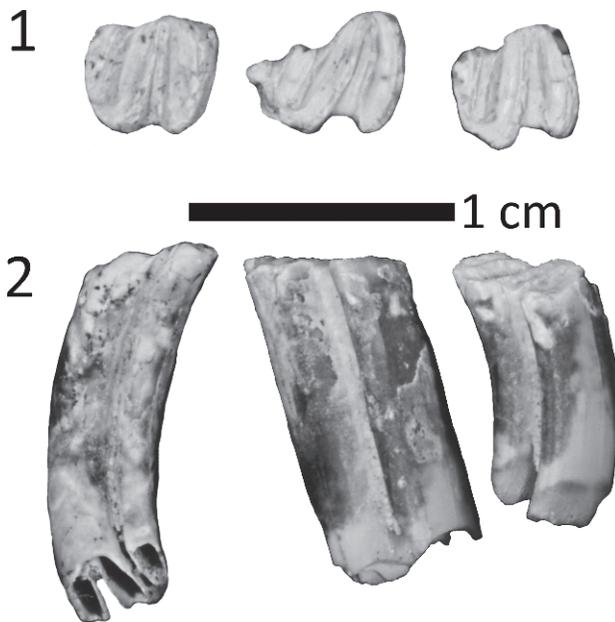| Locality		m1AP	m1T	m2AP	m2T
Rattlesnake, OR	JODA 13984	8.11	8.23	8.25	7.70
Hagerman, ID (N=10)	mean (st. dev.)	8.28 (0.42)	8.34 (0.47)	8.14 (0.43)	8.02 (0.64)
Jackass Butte, ID[1] (N=4)	mean (st. dev.)	7.55 (0.37)	8.20 (0.62)	7.13 (1.00)	7.47 (0.67)

[1] From Shotwell, 1970.

FIGURE 3—Right M1 or M2, left p 4, left m1 or m2 of *Dipoides stirtoni* (Wilson, 1934) from the late early Hemphillian-aged Rattlesnake Formation, Oregon: *1*, JODA 14098 occlusal view; *2*, labial view.

and magnetostratigraphy, indicates a late early Hemphillian age, between 7.3 and 7.05 Ma. The presence of *Dipoides stirtoni*, a characteristic early Hemphillian species, supports this inferred age. This record from the Rattlesnake Formation indicates *Castor* had arrived in North America by at least 7.05 Ma, and possibly earlier.

The timing of *Castor*'s immigration to North America in the late early Hemphillian corresponds with the arrival of several carnivores, including: a bear (*Indarctos*, Pilgrim, 1913), a grison (*Lutravus*, Furlong, 1932), and an ailurid (*Simocyon*, Wagner, 1858) (Woodburne, 2004). These three carnivores have all been found in the Rattlesnake Formation (Merriam et al., 1916, 1925; Thorpe, 1921). Early records of immigrant taxa in Hemphillian faunas from Oregon are not surprising given its geographic location, including some of the closest Hemphillian sites to the land bridge between North America and Asia (Shotwell, 1956).

Castor and members of the subfamily Castoroidinae repeatedly co-occur in the fossil records of North America, Europe, and Asia. The presence of both *C. californicus* and *Dipoides stirtoni* in the Rattlesnake Formation is similar to what is seen in the Rome Formation of southeastern Oregon (Wilson, 1937). As in the Rattlesnake and Rome Formations, *Castor* and *Dipoides* species are found together at other Hemphillian sites across North America, including the pits of *Pliohippus* Draw from the Snake Creek formation in Nebraska (Stirton, 1935), as well as the McKay Reservoir, Arlington, and Ordnance localities in Northern Oregon (Martin, 2008). *C. californicus* co-occurs with *D. rexroadensis* (Hibbard and Riggs, 1949) in the early Blancan White Bluffs Local Fauna from the Ringold Formation of Washington (Gustafson, 1978). Another early Blancan locality in northeastern Oregon, the Always Welcome Inn Local Fauna, has *C. californicus* and *Dipoides* sp. (Van Tassell et al., 2007). In the early to mid-Blancan Glenns Ferry Formation of Hagerman, *C. californicus* co-occurs with the similar sized *Procastoroides intermedius* (formerly assigned to *Dipoides*) (Zakrzewski, 1969).

After the immigration of *Castor* to North America, changes in the morphology and abundances of *Castor* and castoroidine beavers may reflect niche partitioning by these lineages.

Both *Castor* and *Dipoides* show adaptations for semi-aquatic locomotion (Samuels and Van Valkenburgh, 2008), an herbivorous diet of highly abrasive material (Stirton, 1947; Samuels, 2009), and tree-cutting behavior (supported by artifactual evidence, see Rybczynski, 2007, 2008).

Dipoides is relatively common in the Rattlesnake Formation, while *Castor* is only known from a single find. The relative abundances of these two species are similar in Hemphillian localities from northern Oregon, where *Castor* is rare and *Dipoides* is common (Martin, 2008). This may be a consequence of *Castor*'s recent immigration to the area, or environmental conditions that favored the significantly smaller *Dipoides* (Martin, 2008). In the mid-Blancan at Hagerman the situation is reversed, *C. californicus* is particularly abundant throughout the section, while *Procastoroides intermedius* (Zakrzewski, 1969) is much rarer. These two were of similar size and locomotor habits (Samuels and Van Valkenburgh, 2008), and thus may have competed more directly, with their abundances reflecting competition or environmental conditions that favored *Castor*.

From the Miocene through the Pleistocene of North America, *Castor* seems to have gotten slightly smaller (Stirton, 1935; Shotwell, 1970) but otherwise changed little morphologically (Martin, 1989). Over this same time span, members of the Castoroidinae got progressively larger (Shotwell, 1955; Martin, 1989) and show corresponding increases in adaptation for aquatic locomotion, showing limbs more specialized that any extant semi-aquatic rodent (Samuels and Van Valkenburgh, 2008). Rybczynski (2008) found *Castor* and castoroidine beavers, including *Dipoides*, to have differences in incisor shape and wood-cutting performance that suggest the types of trees each group favored may have been different. These differences in dietary preference, along with differences in locomotor adaptations and body size, may have allowed these beaver species to partition niches and avoid competition.

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APPENDIX *1*—Measurements (in mm) of *Castor californicus* teeth; AP=anteroposterior length, T=transverse breadth.

Specimen	Locality	m1AP	m1T	m2AP	m2T
JODA 13984	Rattlesnake, OR	8.11	8.23	8.25	7.70
HAFO 792	Hagerman, ID	8.84	8.48	8.17	8.34
HAFO 1022	Hagerman, ID	8.68	8.06	8.35	8.03
HAFO 1108	Hagerman, ID	8.19	8.64	8.05	8.81
HAFO 2244	Hagerman, ID	8.08	8.22	8.5	8.09
HAFO 5937, 5938	Hagerman, ID	8.37	8.71	8.06	8.66
HAFO 8509	Hagerman, ID	8.18	9.24	8.21	8.86
IMNH 32324	Hagerman, ID	8.61	8.14	8.00	7.13
IMNH 32325	Hagerman, ID	8.58	8.36	8.47	7.50
IMNH 32326	Hagerman, ID	7.78	7.53	8.55	7.37
NMNH 26154	Hagerman, ID	7.50	7.98	7.07	7.43
UOMNH 16336	Jackass Butte, ID[1]	7.7	8.4	7.5	7.8
UOMNH 16337	Jackass Butte, ID[1]	7.0	7.3	6.0	6.7
UOMNH 16338	Jackass Butte, ID[1]	7.8	8.7	7.9	7.9
UOMNH 17436	Jackass Butte, ID[1]	7.7	8.4	—	—

[1] From Shotwell, 1970.