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The Last Fossil Primate in North America, New Material of the Enigmatic *Ekgmowechashala* From the Arikareean of Oregon

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KEY WORDS Ekgmowechashalinae; Adapiformes; John Day Formation

ABSTRACT **OBJECTIVE:** Primates were common in North America through most of the Eocene, but vanished in the Chadronian, about 35 million years ago. In the Arikareean, about 6 million years later, the enigmatic primate *Ekgmowechashala* appeared in the Great Plains and Oregon. This taxon shows little resemblance to other North American primates and its phylogenetic position has long been debated. New material of this taxon allows a revised assessment of its age and how it is related to other primates. **METHODS:** Recently collected *Ekgmowechashala* specimens from the Turtle Cove Member of the John Day Formation in Oregon are described. These specimens are compared to previously collected material from South Dakota and Nebraska, as well as other fossil primates from North America and Asia. **RESULTS:** Study of the John Day material allows diagnosis of a new, distinct species. Comparison of *Ekgmowechashala*

to a pair of recently described Asian primates, *Muangthanhinius* and *Bugtilemur*, suggests that it is a strepsirrhine adapiform, rather than an omomyid. The well-defined stratigraphy and dated marker beds of the Turtle Cove Member provide a refined age for *Ekgmowechashala* occurrences in Oregon, during the Oligocene (early Arikareean).

CONCLUSIONS: The age and morphology of these ekgmowechashaline taxa suggest that the group originated in Asia and dispersed to North America in the Oligocene, after the extinction of other primates in North America. Contemporaneous occurrences of *Ekgmowechashala* in Oregon and the Great Plains indicate the last non-human primates vanished in North America about 26 million years ago. *Am J Phys Anthropol* 158:43–54, 2015. © 2015 Wiley Periodicals, Inc.

During the Eocene, the earth was in a ‘greenhouse’ state free from permanent ice sheets (Zachos et al., 2001). Euprimates first appeared in North America during the early Eocene (Bown and Rose, 1987; Smith et al., 2006; Beard, 2008) and much of North America was inhabited by primates through the middle Eocene (Gunnell et al., 2008). During the late middle Eocene (42–37 Ma) global climate conditions changed dramatically. In North America, this resulted in a shift from semi-tropical closed canopy forests to more open woodland and savannah habitats, and a corresponding decrease in primate diversity (Storer, 1990; Janis, 1993; Wing, 1998; Gunnell et al., 2008; Townsend et al., 2010). Multiple primate taxa survived into the Duchesnean, but only the omomyid *Rooneyia* from Texas and *Chumashi* survived into the early Chadronian (late Eocene) (Wilson, 1966; Ostrander, 1987). After the extinction of *Rooneyia* and *Chumashi* almost 35 million years ago, primates were absent from North America for about 6 million years, until the appearance of the enigmatic *Ekgmowechashala* in the early Arikareean (MacDonald, 1963, 1970; Rose and Rensberger, 1983).

Ekgmowechashala was originally known from nine dentary specimens from the Upper Sharps Formation of South Dakota (MacDonald, 1963, 1970; Szalay, 1976), but a maxilla fragment with teeth from the John Day Formation of Oregon was later assigned to this taxon (Rose and Rensberger, 1983). This rare primate has also been noted from the contemporaneous Gering Formation of Nebraska and Turtle Butte Formation of South Dakota (Swisher, 1982; Schumaker, 2008; Martin, 2011).

The phylogenetic position of this taxon has been long debated, with various authors placing *Ekgmowechashala* in the Omomyidae (Primates) (MacDonald, 1963, 1970; Szalay, 1976; Szalay and Delson, 1979; Rose and Rensberger, 1983; Gunnell et al., 2008), Plagiomenidae (Dermoptera) (McKenna, 1990), and most recently in the Adapiformes (Primates) (Ni et al., 2010).

John Day Formation strata in the Sheep Rock area (Fig. 1) have been studied for about 150 years. The best known assemblage from that area is the Oligocene aged Turtle Cove fauna, which includes nearly 100 recognized mammal species (Fremd, 2010). In 1997, the first stratigraphically assignable specimen of *Ekgmowechashala*, a left m1, was

Additional Supporting Information may be found in the online version of this article.

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recovered from Turtle Cove unit H, a stratum containing early Arikareean (Ar1) fauna. After more than a decade of diligent searching, the exact same site yielded two additional specimens, a p4 and m3, in 2011. And in early 2015 a dentary fragment that fits the p4 and m1 was discovered, confirming that these teeth are from the same individual. In 2013 and 2014, two other partial m1s were collected from a second site on Sheep Rock, also within unit H. The well-defined stratigraphy and a series of dated marker beds at these sites allow us to place these new specimens of *Ekgmowechashala* in a chronological and biostratigraphic context. Study of these new specimens confirms the presence of *Ekgmowechashala* in Oregon, facilitates direct comparison to specimens from the Great Plains, and refines the age of occurrence of the last non-human primate in North America.

MATERIALS AND METHODS

The specimens newly described here are all housed in the collection of John Day Fossil Beds National Monument. Comparisons made in this article are based primarily on study of casts of fossils at other institutions, supplemented by published photographs and drawings. Dental nomenclature used in comparative descriptions follows that of Szalay (1976) and a labeled illustration is included as a Supporting Information figure (Fig. S1). Upper teeth are designated by capital letters and lower teeth by lower-case letters (e.g., M1 and m1). Measurements represent maximum lengths and widths taken at the occlusal surface. These measurements were taken using Mitutoyo Absolute digital calipers to the nearest 0.01 mm. Precise locality information for recent collections, including GPS (global positioning satellite) data, is on file at John Day Fossil Beds National Monument. Abbreviations for institutions: JODA, John Day Fossil Beds National Monument; LACM, Natural History Museum of Los Angeles County; SDSM, South Dakota School of Mines and Technology, Museum of Geology; UCMP, University of California Museum of Paleontology.

GEOLOGICAL SETTING

Distributed widely throughout central and eastern Oregon, the John Day Formation includes ~1000 m of geographically variable strata, consisting mainly of volcanoclastic sedimentary rocks and airfall tuffs (Fisher and Rensberger, 1972; Robinson et al., 1984; Retallack et al., 2000; Albright et al., 2008; McClaughry et al., 2009). These strata are well understood after extensive study for more than 100 years (Merriam, 1901; Hay, 1963; Fisher and Rensberger, 1972; Fremd et al., 1994; Hunt and Stepleton, 2004; Albright et al., 2008). A series of conspicuous marker units and distinctive lithologies of layers throughout the sequence have allowed exposures in Oregon to be correlated at great distances (Albright et al., 2008).

Three distinct “facies” of the John Day Formation have been described: western, southern, and eastern (Robinson et al., 1984). A nearly continuous sequence of strata is exposed within outcrops of the eastern “facies,” preserved in the vicinity of the Sheep Rock Unit of John Day Fossil Beds National Monument. The recent work of Hunt and Stepleton (2004) and Albright et al. (2008) have produced a detailed litho- and chronostratigraphy for the John Day Formation, which is paired with radiometric and paleomagnetic calibration (Albright et al., 2008; figs. 9 and 10). As currently recognized, the John Day Formation includes seven members, ranging from

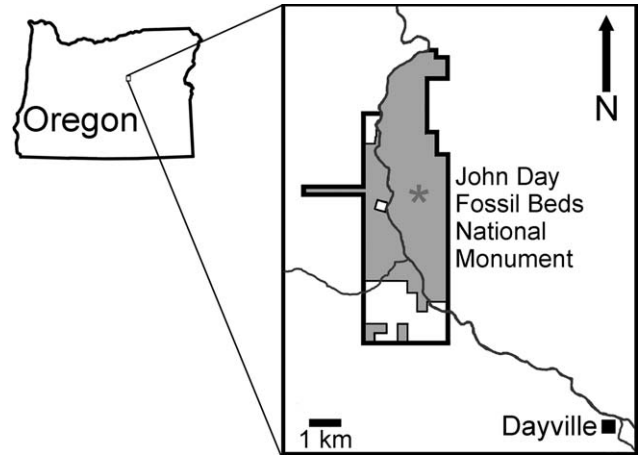


Fig. 1. Map showing the Sheep Rock Unit of John Day Fossil Beds National Monument, Grant County, Oregon. The asterisk indicates the location of Sheep Rock, where the specimens described here were found.

middle Eocene to early Miocene in age, about 39 to 18 Ma (Hunt and Stepleton, 2004; Albright et al., 2008).

All of the specimens described here originate from within the Turtle Cove Member of the John Day Formation (Fig. 2), which is characterized by lithology consisting of zeolitized bluish-green and tan claystones and siltstones (Fisher and Rensberger, 1972). Fremd et al. (1994) subdivided the Turtle Cove Member and the overlying Kimberly Member into lithostratigraphic units A–M, based on the individual lithologies of beds and interspersed tuffs. There are currently 12 radiometric dates from the John Day Formation, including six tuffs within the Turtle Cove Member alone. These tuffs were radiometrically dated using $^{40}\text{Ar}/^{39}\text{Ar}$ single-crystal laser-fusion (Albright et al., 2008). The radiometric dates relevant to this study are the following: Picture Gorge Ignimbrite (Member H of Robinson) dated 28.7 ± 0.07 Ma, Deep Creek Tuff dated 27.89 ± 0.57 Ma, Biotite Tuff dated 27.14 ± 0.13 Ma, and Tin Roof Tuff dated 25.9 ± 0.3 Ma (Albright et al., 2008).

SYSTEMATIC PALEONTOLOGY

Order Primates Linnaeus, 1758
 Semiorder Euprimates Hoffstetter, 1977
 Suborder Strepsirrhini Geoffroy Saint-Hilaire, 1812
 Infraorder Adapiformes Hoffstetter, 1977
 Family Incertae Sedis
 Subfamily Ekgmowechashalinae Szalay, 1976
 Genus *Ekgmowechashala* Macdonald, 1963

Type species

Ekgmowechashala philotau

Included species

Ekgmowechashala zancanellai, new species

Emended diagnosis

Teeth are low crowned with bulbous cusps and weakly developed cristae; upper and lower molars decrease in size distally; P4 and p4 molarized; double-rooted p2; p4 with enlarged talonid, metastylid, ectostylid, and several small cusps; trigonids of lower molars mesiodistally

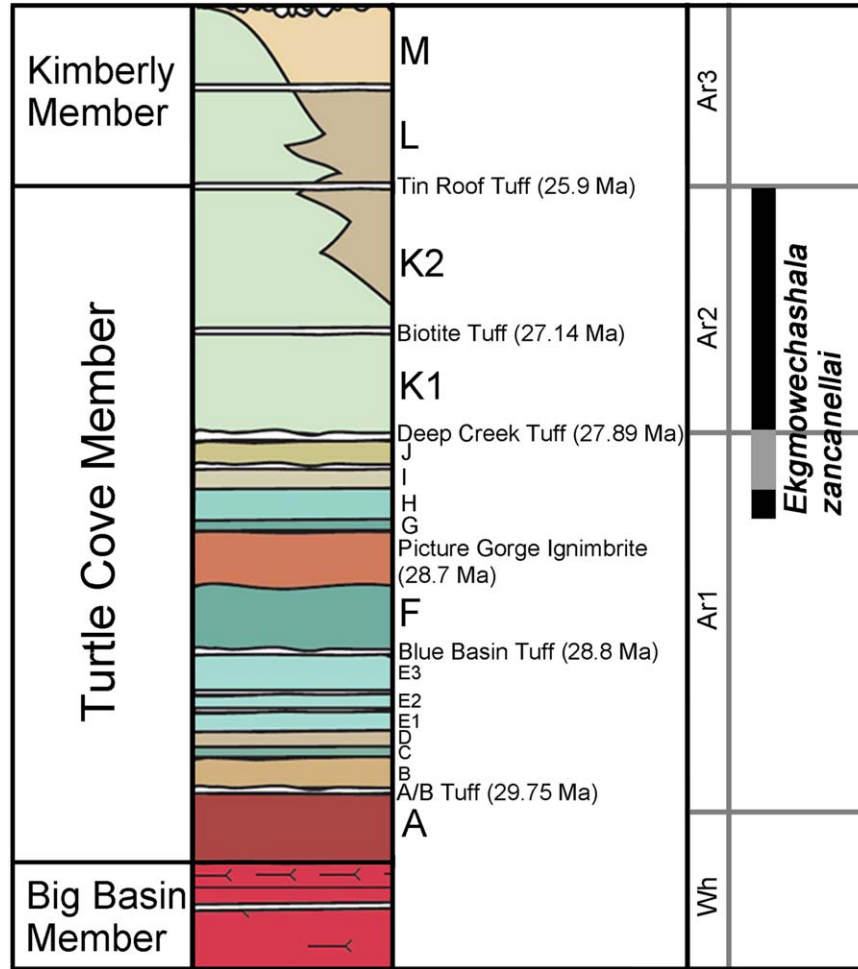


Fig. 2. Composite stratigraphic section of the John Day Formation near Sheep Rock with stratigraphic position of the known *Ekgmowechashala* specimens. Stratigraphy and radiometric dates are based on Albright et al. (2008) and Fremd (2010). The black bar indicates confirmed or inferred stratigraphic ranges; grey bar indicates range-through. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

compressed; paraconids absent and paracristids weak to absent in lower molars; lower molar hypoconulids distinct, twinned with hypoconid; P4 with distally displaced paracone and large paraconule, located mesial to and between protocone and paracone; prominent parastyle present in P4 and M1; M1 and M2 with large pseudohypocone arising from the “*Nannopithec*-fold” of the protocone; tooth enamel crumpled.

Distribution

Early Arikareean (early? and late Oligocene, Ar1 and Ar2) of South Dakota, Nebraska, and Oregon.

New species

Ekgmowechashala zancanellai new species (Figs. 3–6)

Type specimen

JODA 6322, left dentary fragment with p4, m1, and m3 (Figs. 3–4).

Referred specimens

UCMP 128231, left maxilla with P4, M1, and partial M2; JODA 16525, partial left m1; JODA 16526, partial left m1.

Horizon and locality

JODA 6322, 16525, 16526 – JDNM 8, Sheep Rock, Grant County, OR, Unit H, Turtle Cove Member, John Day Formation; UCMP 128231 – UCMP V82379, Grant County, OR, unknown unit, upper Turtle Cove Member, John Day Formation.

Age

Early Arikareean (early? and late Oligocene, Ar1 and Ar2), between Picture Gorge Ignimbrite dated 28.7 ± 0.07 Ma and Tin Roof Tuff dated 25.9 ± 0.3 Ma (Albright et al., 2008).

Diagnosis

p4 paracristid more distinct than in *E. philotau* and located just lingual to midline of tooth; proportions of lower dentition distinct from *E. philotau*, m1 substantially enlarged and m3 reduced relative to other cheek teeth; m3 paracristid distinct and broad, enclosing a small trigonid basin.

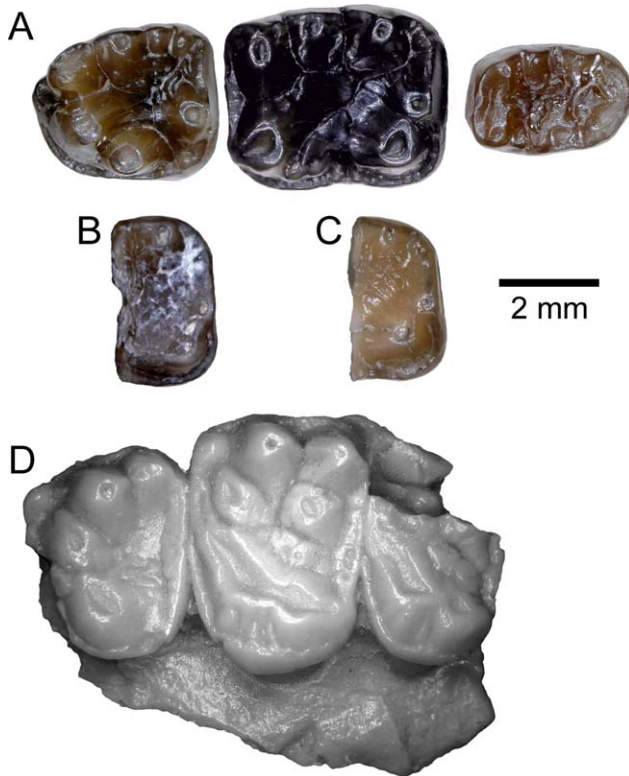


Fig. 3. *Ekgmowechashala* specimens from the Arikareean of Oregon. **A.** JODA 6322, holotype of *Ekgmowechashala zancanelloi*, left p4, m1, and m3; **B.** JODA 16525, partial left m1; **C.** JODA 16526, partial left m1; **D.** grayscale cast of UCMP 128231, left maxilla with P4, M1, and partial M2. Scale bar equal 2 mm. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

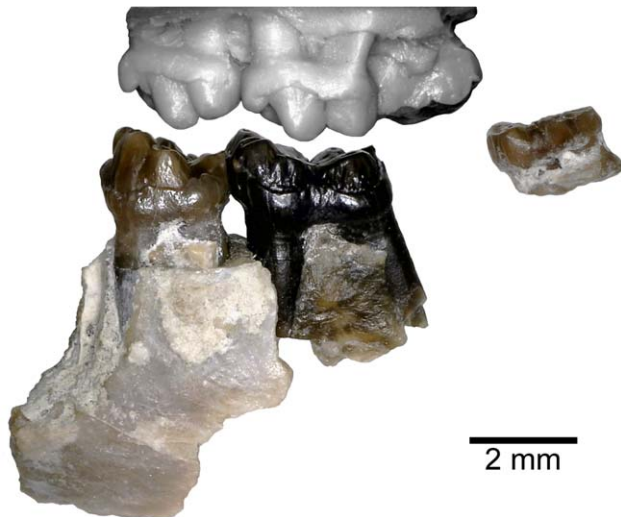


Fig. 4. Occlusion of upper and lower dentitions of *Ekgmowechashala zancanelloi* from Oregon, in lateral view. Illustrated above is the maxillary dentition of UCMP 128231 (grayscale cast) and below is the mandibular dentition of JODA 6322, both in lateral view. Scale bar equals 2 mm. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

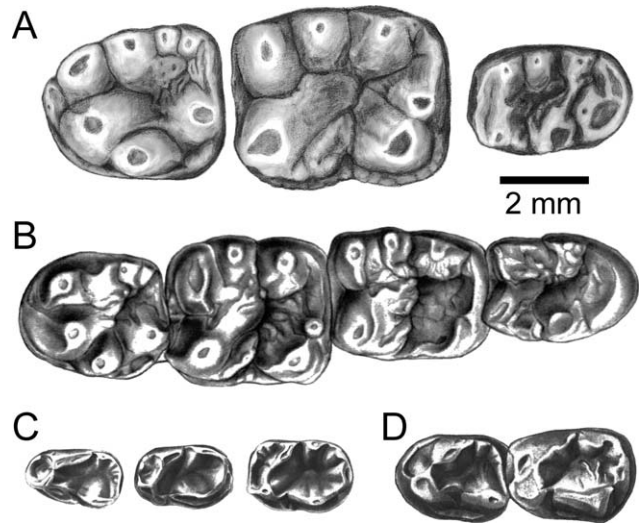


Fig. 5. Comparison of lower dentition among known ekgmowechashaline primates. **A.** *Ekgmowechashala zancanelloi*, JODA 6322, left p4, m1, and m3; **B.** *E. philotau*, composite lower dentition (p2 to m3) based on SDSM 5550, SDSM 61204, and LACM 9207; **C.** *Bugtilemur mathesonae*, UMC-DBC 2139, left p3, UMC-DBC 2143, left p4, UMC-DBC 2141, left m1, UMC-DBC 2161, left m2; **D.** *Muangthanhinius siami*, TF 6212, left dentary with p4 to m1. Scale bars equal 2 mm. Illustrations adapted from the following sources: *E. philotau*, Szalay (1976:Fig. 133); *B. mathesonae* copyright © by Laurence Meslin-CNRS, Marivaux et al. (2001, fig. 2); and *M. siami* © by Laurence Meslin-CNRS, Marivaux et al. (2006, fig. 3). Reproduced by permission of Laurence Meslin. Original illustration of *E. zancanelloi* by Keila Bredehoeft. © Reproduced by permission of Laurence Meslin.

Etymology

Patronym for Bureau of Land Management archeologist John Zancanella, who discovered the type specimen and whose dedicated paleontological efforts helped to discover and preserve many important localities in central and eastern Oregon.

DESCRIPTION

While represented by limited material, the lower teeth of the holotype of *Ekgmowechashala zancanelloi* (JODA 6322, Fig. 3) are complete and well-preserved enough to distinguish them from *E. philotau*. As is characteristic of the genus, the teeth display low, bulbous cusps and weakly developed cristae, with well-developed irregular cingulids. The enamel of both the p4 and molars is crenulated, particularly within the talonid basin and on the surfaces of some cusps.

The p4 of JODA 6322 is semimolariform and nearly rectangular in shape with a low, irregular cingulid surrounding the mesial and buccal borders of the tooth. There is no paraconid, but a small, distinct paracristid is present just lingual to the midline of the tooth, mesial to and between the protoconid and metaconid. A small trigonid basin lies distal to the paracristid, formed primarily by the relatively large buccally located protoconid and mesiolingually located metaconid. Distobuccal to the protoconid is a large ectostylid (ectostylar cusp of Rose and Rensberger, 1983), nearly equal in size to the protoconid. Distal and lingual to this stylid is the hypoconid, which has a pair of crests extending from it. One crest extends buccally from the hypoconid and connects to the distal

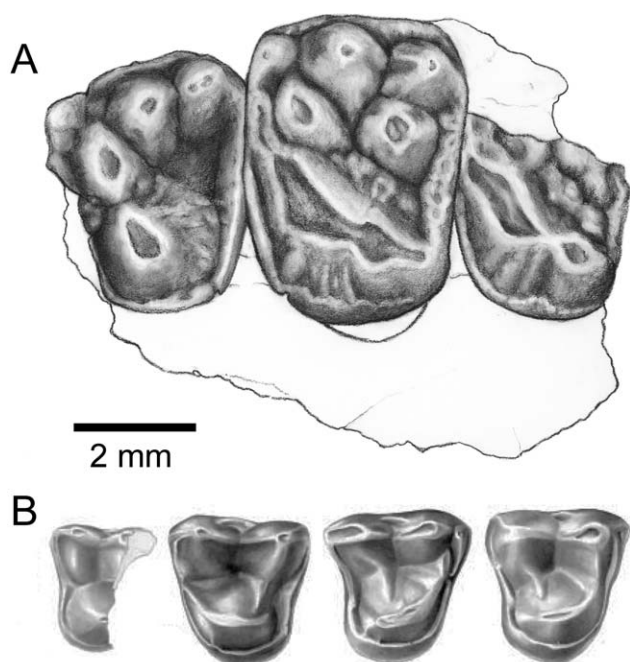


Fig. 6. Comparison of upper dentition among known ekgmowechashaline primates. **A.** *Ekgmowechashala zancanellai*, UCMP 128231, left maxilla with P4, M1, and partial M2; **B.** *Bugtilemur mathesonae*, UMC-DBC 2147, partial right P4, UMC-DBC 2151, left M1, UMC-DBC 2146, right M2, and UMC-DBC 2152, right M2. Scale bars equal 2 mm. Illustration of *B. mathesonae* copyright © by Laurence Meslin-CNRS adapted from Marivaux et al. (2001, fig. 2). Reproduced by permission of Laurence Meslin. Original illustration of *E. zancanellai* by Keila Bredehoeft. © Reproduced by permission of Laurence Meslin.

surface of a small, but distinct cuspule in the distobuccal corner of the tooth; the other crest (postcristid) extends lingually from the hypoconid to the distolingual corner of the tooth. Along the buccal cingulid between the distobuccal cuspule and the ectostylid is another small cingular cuspule. Distal to the metaconid is a relatively large metastylid, which is well-separated from both the metaconid and entoconid. Just distal to the metastylid on the lingual border of the p4 is a much smaller entoconid. Also located on the lingual border of the p4 distal to the entoconid and mesiolingual to the lingual extension of the postcristid is an additional small neomorphic cuspule, nearly equal in size to the entoconid.

The m1 of JODA 6322 is rectangular in occlusal outline, with an enlarged talonid basin. As in the p4, the m1 has no paraconid. The mesial end of the tooth has a large buccal protoconid and lingual metaconid; the protoconid between these cusps is rather poorly developed. A flat precingulid runs along the surface mesial to the protoconid and metaconid, possibly representing a remnant of the paracristid. The protoconid has a small mesial crest that may be a remnant of the paracristid, as well as a distal crest that extends distolingually from its distobuccal corner, and which bears a pair of small cuspules. The metaconid is mesiodistally compressed and nearly equal in size to the protoconid. Distal to the metaconid is a large, bulbous metastylid. Distal to the metastylid is a similarly sized entoconid, nearly located in the distolingual corner of the tooth. The talonid basin is enlarged and open buccally between the distal crest of

the protoconid and the hypoconid. The hypoconid is crescentic in shape and bears a very weakly developed cristid obliqua, which runs mesially from the hypoconid along the buccal margin of the tooth. Distolingual to the hypoconid is a smaller, closely appressed hypoconulid. Extending lingually from the hypoconulid is the postcristid, which extends and connects to the distolingual corner of the entoconid. A prominent irregular cingulid extends from the mesiobuccal edge of the protoconid along the buccal margin of the m1 and wraps around the distal surface of the hypoconid.

Two partial m1s are included in the JODA collection, JODA 16525 and 16526. Both preserve only the distal part of the tooth, including the entoconid, hypoconid, hypoconulid, and part of the talonid basin. The talonid basins of both specimens are distinctly crenulated, as is characteristic of *Ekgmowechashala* (Macdonald, 1963; Gunnell et al., 2008). These teeth are identified as m1 rather than m2 based on the fact that the hypoconulid is relatively prominent and distinct from the hypoconid, while the m2 hypoconulid is simply a small projection from the distal cingulid of the hypoconid (McKenna, 1990). Both specimens are substantially smaller than JODA 6322, with JODA 16525 10% and JODA 16526 nearly 13% smaller (Table 1).

The m3 of JODA 6322 is elongate, with a rather distinctive arrangement of cusps. As in the m1 and m2, there is no paraconid, though the paracristid is much more distinct and substantial than in the other molars, running transversely across the entire mesial end of the m3. There is a mesiodistally narrow, transversely oriented trigonid basin between the paracristid and the protoconid and metaconid. The protoconid and metaconid are nearly equal in size and are connected via a much more prominent protocristid than is present in the m1. A small crest extends distally from the protoconid; this crest bears a small cuspule as in the m1. The metaconid is mesiodistally compressed and has a distinct buccally directed crest that joins the protocristid. The metastylid is smaller than the metaconid and just distal to it, and well separated from the similarly sized entoconid. The hypoconid is large and located more mesially than in the anterior molars, mesial to the entoconid, yielding a substantially smaller talonid basin. A low crest runs distolingually from the hypoconid to the entoconid. The hypoconid is separated distally from the similarly large hypoconulid. Extending from the hypoconulid across the distal surface of the m3 is a broad, crescent-shaped postcristid. The postcristid extends to the distolingual corner of the tooth, just distal to the entoconid. The distal part of the m3 is relatively worn, resulting in large concavities in the surfaces of the hypoconid and hypoconulid.

Upper dentition of UCMP 128231 (Fig. 3) was previously described in detail by Rose and Rensberger (1983), and the specimen was referred to *Ekgmowechashala* sp. based on details of dental morphology and proper occlusion of the specimen with a specimen of *Ekgmowechashala philotau* (SDSM 62104) from South Dakota. The description that follows is based mainly on the description of Rose and Rensberger (1983), with some modifications based on more recent studies. The teeth in this specimen are characterized by bulbous cusps, weakly developed cristae, and well-developed irregular cingula wrapping around the teeth. Crenulated enamel is evident within basins and on unworn surfaces of cusps.

The upper P4 of UCMP 128231 is trapezoidal in shape and semimolariform. The tooth has a large, low

TABLE 1. Measurements (in mm) of *Ekgmowechashala* specimens, some data derived from Macdonald (1963, 1970)

	<i>Ekgmowechashala philotau</i> Wounded Knee fauna, Sharps Fm. South Dakota						<i>Ekgmowechashala zancanellai</i> Turtle Cove fauna, John Day Fm. Oregon			
	SDSM 5550	SDSM 5551	SDSM 55111	SDSM 62104	LACM 9206	LACM 9207	JODA 6322	JODA 16525	JODA 16526	UCMP 128231
p4L	3.3	3.0		3.20		3.49	3.67			
p4W	2.8	2.7		2.73		3.11	3.08			
m1L	3.6	3.5	4.2	3.72	4.17	4.06	4.46			
m1W	3.3	3.3	3.5	3.55	3.35	3.48	3.78	3.41	3.30	
m2L	3.4	3.3	3.9	3.38						
m2W	2.8	2.8	2.8	3.09						
m3L				3.25			3.21			
m3W				2.42			2.29			
P4L										3.35
P4W										4.20
M1L										3.58
M1W										5.21
M2L										3.34 ^a
M2W										4.87 ^a
p4L/m1L	0.917	0.857		0.860		0.860	0.823			
m3L/m1L				0.874			0.720			

^a Approximate based on incomplete teeth and alveoli.

protocone in the mesiolingual corner, no hypocone, and the paracone and metacone are closely appressed. The paracone is larger and higher than the metacone, and lies near the midpoint of the buccal margin. Between and slightly mesial to the protocone and paracone is a prominent paraconule, which is larger but lower than the metacone. A distinct parastyle lies in the mesiobuccal corner of the tooth. The tooth is surrounded by a low, well developed cingulum; the mesial part of the cingulum is broken, while the distal part is broadened and includes several tiny worn cusps. The major cusps (protocone, paraconule, paracone, and metacone) form a semicircle, with a broad posterointernal basin distal to them.

The M1 of UCMP 128231 is larger and more quadrate than the P4. As in the P4, the paracone is near the center of the buccal margin of the tooth, with a distinct parastyle mesial and closely appressed metacone distal to it. The paraconule and metaconule are low and large, lying mesiolingual to the paracone and metacone respectively. The crescentic protocone lies in the mesiolingual corner of the tooth, with an oblique mesiobuccal to distolingual orientation. A narrow crest extends buccally from the paracone, ending adjacent to the parastyle and not connecting to the paraconule. Connected to and extending from the distal edge of the protocone is a prominent mesiodistally oriented "pseudohypocone." This cusp is called a "pseudohypocone" due to the fact that it arises from the "Nannopithec-fold" of the protocone, rather than from the postcingulum (Ni et al., 2010; Anemone et al., 2012). The trigon is closed mesially, but is open distally between the 'pseudohypocone' and metaconule. Like the P4, the M1 is surrounded by a low, well developed cingulum. This cingulum is broad and shelf-like distally, with several worn cusps, and the lingual surface, particularly adjacent to the protocone, is irregular and "vaguely beaded" (Rose and Rensberger, 1983).

The M2 of UCMP 128231 is incomplete, with the buccal half missing. The preserved lingual portion of the M2 is mesiodistally narrower than the M1, and the alveoli preserved in the maxilla indicate the tooth was also transversely narrower. The M2 protocone and pseudohypocone are similar in shape to the M1. These cusps are less worn than in the M1, revealing the cusps are

closely appressed but distinct. The enamel of the basin buccal to the protocone and pseudohypocone is heavily crenulated.

As indicated by Rose and Rensberger (1983), the distally displaced paracone of *Ekgmowechashala* is unique among primates. The paracone of the P4 occludes mesially with the distal surface of the p4 protoconid and lingual surface of the p4 ectostylid (Fig. 4). Similarly, the M1 paracone occludes mesially with the distal surface of the m1 protoconid and mesial surface of the hypoconid (Fig. 4). Worn surfaces of cusps have exposed dentine; this wear is more substantial in the lingual cusps of the upper teeth. Comparison of the M2 to P4 and M1 reveals enamel crenulation in the upper cheek teeth was substantial, though reduced with wear. Similar comparison of several m1 specimens shows extensive crenulation is present in the talonid basin and surfaces of cusps in unworn teeth (JODA 16526), but crenulation was reduced with wear (JODA 6322 and 16525) (Fig. 3).

COMPARISONS

The dentition of *Ekgmowechashala* is unusual among primates. In both the upper and lower dentitions, the molars decrease in size posteriorly. The P4 is semimolariform with a distinct metacone. The upper molars are characterized by bulbous cusps and well developed basins, and bear a prominent "pseudohypocone." The p4 is semimolariform with a prominent ectostylid between and buccal to the protoconid and hypoconid. The lower molars are broad and low crowned, the paraconid is absent and a large metastylid present, and the talonid basin is enlarged and shallow. Crests in the upper and lower molars, including the cristid obliqua, are poorly defined, suggesting that shearing was not well developed. In both the upper and lower dentition of *Ekgmowechashala*, the enamel is crenulated.

The John Day *Ekgmowechashala* specimens show some morphological and proportional differences from previously described material of *E. philotau* (Fig. 5, Table 1). While the range of variation in that rare taxon is unknown, the Oregon specimens are distinct from material from the Great Plains. The p4 paracristid

of *E. zancanellai* is prominent and much larger than that of *E. philotau*, where it is nearly absent. All molars in *E. philotau* show a highly reduced paracristid, merely present as a small precingulid mesial to the protoconid and metaconid. In *E. zancanellai*, the m3 paracristid is a distinct, broad ridge running across the entire mesial end of the tooth, yielding a much larger m3 trigonid than is present in *E. philotau*. The molars of *Ekgmowechashala* decrease in size posteriorly, and the proportions of the molars of *E. zancanellai* are distinct from *E. philotau*. While the size of the p4 is relatively similar in both species, the m1 is enlarged and the m3 is dramatically reduced in *E. zancanellai* (Table 1); in SDSM 61204 the m3 is 87% the length of the m1, but in JODA 6322 the m3 is only 72% the length of the m1.

The new specimens of *Ekgmowechashala* from Oregon, as well as some recent discoveries from Asia, facilitate re-evaluation of this species' relationships to other primates. Despite the unusual morphology of *Ekgmowechashala*, it has traditionally been placed within the Omomyidae (Macdonald, 1963, 1970; Szalay, 1976; Szalay and Delson, 1979; Rose and Rensberger, 1983; Szalay and Lucas, 1996; Albright, 2005; Gunnell et al., 2008). This placement was based on the presence of lower molars with the hypoconulid displaced toward the hypoconid, and upper molars with a well-developed "hypocone" (identified as a 'pseudohypocone' by Ni et al., 2010) and conules located in the buccal half of the teeth.

Szalay (1976) suggested that the origin of *Ekgmowechashala* may be in an omomyid like *Rooneyia viejaensis*. Like *Ekgmowechashala*, *Rooneyia* has cheek teeth with bulbous cusps. However, in *Rooneyia* the P4 metacone is absent, as is typical of most omomyids other than *Shoshonius* (Szalay, 1976). *Shoshonius* lacks the P4 paraconule, and it also has a small hypocone and a large mesostyle in the upper molars, unlike *Ekgmowechashala*. The prominent hypocone of the upper molars in *Rooneyia* and *Washakius* arises from the distal cingulum, unlike that of *Ekgmowechashala* (McKenna, 1990; Ni et al., 2010).

Noting differences from omomyids, McKenna (1990) reevaluated *Ekgmowechashala* and referred it to the Plagiomenidae. Various problems with this assessment were indicated by Szalay and Lucas (1996), as well as Gunnell et al. (2008) and Ni et al. (2010). While relation to plagiomenids is not supported, the dissimilarities of *Ekgmowechashala* to known omomyids noted by McKenna (1990) are valid. *Ekgmowechashala* has a number of features that clearly separate it from omomyids, some of which have long been recognized (Szalay, 1976; McKenna, 1990). Unlike known omomyids, *Ekgmowechashala* has: 1) molars that decrease in size distally, 2) molarized fourth premolars (p4 and P4), 3) enlarged canines, 4) double-rooted p2, 5) paraconids of lower molars absent, 6) hypoconulids of lower molars distinct, rather than a mere bulge in the postcristid, 7) large bulbous parastyles of upper P4 and M1, and 8) large "pseudohypocone" in M1 and M2 arising from the "Nannopithec-fold" of the protocone rather than the distal cingulum (Ni et al., 2010).

The combination of characters present in *Ekgmowechashala* suggests that it is not an omomyid, and several recent studies have placed it among the adapiforms (Marivaux et al., 2006; Seiffert, 2007; Ni et al., 2010). As evidenced by SDSM 62104 and LACM 9207, the canine of *Ekgmowechashala* is relatively enlarged (Macdonald, 1970; Szalay, 1976); canine enlargement is common in

adapiforms (Gingerich, 1995; Gunnell et al., 2008). The double-rooted p2 observed in *Ekgmowechashala* is only observed in some adapiforms and stem primates, and seen in no known haplorhines (Ni et al., 2010). Similarly, the distal premolars of many adapiforms are semimolariform and both the p4 and P4 of *Ekgmowechashala* are molarized. As is the case for *Ekgmowechashala*, in adapiforms the talonid basins of the lower molars are typically broad and enamel is often crenulated (Gunnell et al., 2008), though it is worth noting this is also the case for large late occurring omomyines like *Macrotarsius*, *Ourayia*, *Mytonius*, and *Chipetaia*. The m3 of *Ekgmowechashala* has a particularly broad third lobe, which is often the case among adapiforms (Gunnell et al., 2008). As pointed out by Ni et al. (2010), the large "pseudohypocone" in the upper molars of *Ekgmowechashala* arises from the "Nannopithec-fold" (postprotocingulum) of the protocone, which is found in some adapiforms (Simons, 1962; Rose, 2006).

Two recently described primates from Asia, *Bugtilemur mathesoni* and *Muangthanhinus siami* (Marivaux et al., 2001, 2006; Figs. 5–6), are similar to *Ekgmowechashala* and were recently assigned to the *Ekgmowechashalinae* (Seiffert, 2007). Both *Bugtilemur* and *Muangthanhinus* have a molarized p4, reduced or absent p4 paraconid and hypoconulid, mesiodistally compressed molar trigonids, reduced or absent molar paraconids, distinct molar hypoconulids and entoconids, and lateral cristid obliqua (Fig. 5). All three taxa have crenulated enamel in basins, but the crenulation in *Ekgmowechashala* is more substantial, covering much of the tooth surface. Like *Ekgmowechashala*, *Muangthanhinus* has a large canine and double-rooted p2, though no canine or p2 specimens have been reported of *Bugtilemur* (Marivaux et al., 2001, 2006). Like *Ekgmowechashala*, *Bugtilemur* has broad talonid basins and widely separated protoconids and metaconids (Marivaux et al., 2001). Also as like *Ekgmowechashala*, the P4 in *Bugtilemur* is molarized, with a large crescentic protocone and well-developed metacone, and the M1 and M2 bear a distinct parastyle and distally open trigon (Marivaux et al., 2001; Fig. 6).

The cusps of the lower cheek teeth are bulbous and low crowned in *Ekgmowechashala* and *Muangthanhinus*, but more crest-like in *Bugtilemur* (Marivaux et al., 2001, 2006; Fig. 5). While neither of these Asian taxa displays an ectostylid distobuccal to the protoconid, they do have a distinct, laterally positioned postprotoconid ridge. In both *Muangthanhinus* and *Ekgmowechashala*, there are prominent buccal cingulids on the lower p4 and m1. The known material of *Muangthanhinus* suggests that the lower molars decreased in size posteriorly (Marivaux et al., 2006), as is characteristic of *Ekgmowechashala*. In *Bugtilemur*, the m2 is larger than the m1, suggesting the molars did not decrease in size posteriorly (Marivaux et al., 2001). Unlike *Ekgmowechashala*, the M1 and M2 of *Bugtilemur* lack a "pseudohypocone" and conules (Marivaux et al., 2001; Fig. 6).

These two Asian *ekgmowechashalinae* taxa have more distinct paracristids and larger trigonid basins than *Ekgmowechashala* (Fig. 5), though these features are not nearly as large as in most other adapiforms. Additionally, the p4 and m1 of these taxa lack distinct metastylids, but instead show relatively strong postmetacristids. In both *Muangthanhinus* and *Bugtilemur*, the hypoconulids of the lower molars are distinct and in midline position, while this cusp is more buccally

TABLE 2. Estimated body mass (in gm) of *Ekgmowechashala* specimens using the generalized regressions of body mass as a function of tooth area in Gingerich et al. (1982)

	Specimen	Tooth position	Tooth area (ln L x W)	Estimated body mass (g)	95% Confidence interval
<i>Ekgmowechashala zancanellai</i>	JODA 6322	p4	2.425	2191	1997–2404
	JODA 6322	m1	2.825	2342	2172–2526
	JODA 6322	m3	1.995	866	743–1009
	UCMP 128231	P4	2.644	2176	1946–2434
	UCMP 128231	M1	2.926	1737	1555–1941
<i>Ekgmowechashala philotau</i>	SDSM 5550	p4	2.224	1639	1477–1819
	SDSM 62104	p4	2.167	1512	1357–1684
	SDSM 5550	m1	2.475	1391	1267–1526
	SDSM 62104	m1	2.581	1628	1493–1776
	SDSM 55111	m1	2.688	1910	1761–2072
	SDSM 5550	m2	2.253	965	866–1075
	SDSM 62104	m2	2.346	1089	983–1208
	SDSM 55111	m2	2.391	1155	1044–1277
	SDSM 62104	m3	2.062	937	808–1087

Tooth areas were calculated using the data in Table 1.

located and adjacent to the hypoconid in *Ekgmowechashala*. *Muangthanhinius* and *Bugtilemur* have a shallow hypoflexid in the lower molars, due to a large laterally located cristid obliqua extending from the hypoconid to just distal to the protoconid (Marivaux et al., 2001, 2006). In *Ekgmowechashala*, the cristid obliqua is laterally located but very weakly-developed, resulting in a laterally open talonid basin.

The body masses of both *Ekgmowechashala* species were estimated using generalized regressions of body mass as a function of tooth area (Table 2; Gingerich et al., 1982). The mass of *E. zancanellai* was consistent across elements, apart from a relatively low estimate from the m3, which is reduced in that species. Based on the known specimens of *E. zancanellai*, it had a mass of approximately 2100 gm, slightly larger than *E. philotau*. Both *Ekgmowechashala* species were substantially larger than *Muangthanhinius* and *Bugtilemur*, which have estimated masses of 365 and 100 g, respectively (Marivaux et al., 2005; Chaimanee et al., 2013). These two Asian ekgmowechashalines are similar in size to extant dwarf and mouse lemurs (Cheirogaleidae), while *Ekgmowechashala* was more comparable in size to larger species of galagos (*Otolemur crassicaudatus*) and lorises (*Nycticebus bengalensis*). The mass estimates here are similar to that of Rose and Rensberger (1983) and indicate *Ekgmowechashala* was substantially larger than most North American omomyids (Gingerich, 1981), but similar in size to a number of North American and Eurasian adapiforms like *Cantius*, *Smilodectes*, and *Adapis* (Gingerich et al., 1982).

While evidence suggests *Ekgmowechashala* is an adapiform, it and the relatively closely related *Bugtilemur* and *Muangthanhinius* remain of questionable affinities to any of the recognized adapiform primate families without additional material. The distinct hypoconulid in the lower molars of ekgmowechashalines separates them from adapines, cercamoniines, and notharctines, and the relatively buccal position of the hypoconulid (not twinned to entoconid) separates them from sivaladapids (Marivaux et al., 2006). Similarly, the reduced p4 paraconid and hypoconulid of ekgmowechashalines distinguish them from sivaladapines.

An isolated tooth (LSUMG V-2766) from the Toledo Bend local Fauna of Texas was previously referred to

Ekgmowechashala, based on its low crown height and crenulate enamel (Albright, 2005). However, that tooth, identified as a left p4, seems to have a number of characteristics quite distinct from *Ekgmowechashala*. The tooth bears what seems to be a distinct paraconid mesial to and between the protoconid and metaconid, that cusp is consistently absent in the p4 of *Ekgmowechashala*, though a small paracristid remains. Additionally, in the Toledo Bend tooth the styloid distobuccal to the protoconid is smaller and more closely appressed to the protoconid than in *Ekgmowechashala*, and it is well separated from the hypoconid. Additional styloid cusps distal to the entoconid and buccal to the hypoconid of *Ekgmowechashala* are absent in LSUMG V-2766. Unlike the distinct hypoconid and small postcristid of *Ekgmowechashala*, the Toledo Bend specimen has a broad crescentic hypoconid/postcristid occupying the distal part of the tooth. The irregular cingulid wrapping around the mesial and buccal surfaces of the teeth of *Ekgmowechashala* are not present in the Toledo Bend tooth. These differences indicate LSUMG V-2766 is not *Ekgmowechashala* and further study is needed to identify what mammal it represents.

DISCUSSION

Age of *Ekgmowechashala* from Oregon and the Great Plains

The occurrences of *Ekgmowechashala zancanellai* are mapped onto the composite stratigraphic section of the John Day Formation near Sheep Rock in Figure 2. The holotype of *E. zancanellai* (JODA 6322) and two additional specimens from Sheep Rock (JODA 16525, 16526) were recovered from unit H of the Turtle Cove Member of the John Day Formation. The area where these specimens were collected includes a series of well-exposed marker beds, with the Picture Gorge Ignimbrite (28.7 ± 0.07 Ma) below and Deep Creek Tuff (27.89 ± 0.57 Ma) above (Albright et al., 2008). That indicates a well constrained age of between 28.7 and 27.89 Ma for these occurrences, at the end of the early early Arikareean (Ar1) and near the boundary between the early and late Oligocene. The magnetostratigraphic study by Albright et al. (2008) included samples from the Sheep Rock section, placing unit H within magneto-chron C9r.

The *Ekgmowechashala* specimen with upper dentition, UCMP 128231, previously described by Rose and Rensberger (1983) comes from an unknown stratigraphic horizon, but there is sufficient information available to place it in a stratigraphic context with some confidence. The specimen is described as coming from “sediments well above the Picture Gorge Ignimbrite” (Rose and Rensberger, 1983). Furthermore, the specimen is indicated to be associated with specimens of *Allomys nitens*, above the *Meniscomys* Local-Range Zone (Rensberger, 1983), and below the *Pleurolicus* Teilzone (Rensberger, 1973) and *Entoptychus* Concurrent Range Zone (Rensberger, 1971). While Figure 1 in Rose and Rensberger (1983) shows the specimen as occurring above the Deep Creek Tuff, there is no indication of whether or not the Deep Creek Tuff is actually present at the locality from which the specimen was collected, or if this placement is based upon biostratigraphic interpretation.

Recent collections at JODA indicate *Allomys nitens* occurs in units H, K1, and K2 of the Turtle Cove Member of the John Day Formation, as do several species of *Meniscomys*. *Pleurolicus sulcifrons* is restricted to and abundant in units K1 and K2 of the Turtle Cove Member, while *Entoptychus* species appear in the upper portion of unit K2 and dominate collections from the Kimberly and Haystack Valley Member strata (Rensberger, 1971). As UCMP 128231 was found above the Picture Gorge Ignimbrite and with specimens of *Allomys nitens*, that restricts its likely occurrence to the upper part of the Turtle Cove Member, below the Tin Roof Tuff (25.9 ± 0.3 Ma, Albright et al., 2008). Additionally, if the specimen was collected from above the Deep Creek Tuff, then that would suggest it comes from the uppermost part of the Turtle Cove Member, in unit K1 or K2, within the late early Arikareean (Ar2). Depending on the unit from which UCMP 128231 originated, that would place that occurrence between the Deep Creek Tuff (27.89 ± 0.57 Ma) and Biotite Tuff (27.14 ± 0.13 Ma), or Biotite Tuff and Tin Roof Tuff (25.9 ± 0.3 Ma) (Albright et al., 2008).

Ekgmowechashala philotau was originally described from the early early Arikareean (Ar1) Wounded Knee/Sharps Fauna (=Sharps Fauna C) from the Sharps Formation of South Dakota (Macdonald, 1963, 1970). Later, *Ekgmowechashala* was recognized from the early early Arikareean (Ar1) Gering Fauna from the Gering Formation of Nebraska (Swisher, 1982). The upper Sharps Formation and Gering Formation span the same magnetostratigraphic interval as Turtle Cove unit H, magnetochron C9r (Tedford et al., 1996). *Ekgmowechashala* sp. has also been noted from the late early Arikareean (Ar2) aged Turtle Butte Formation of South Dakota (Schumaker, 2008; Martin, 2011). These records confirm the presence of *Ekgmowechashala* in these two regions at the same time, the early Arikareean (Ar1-Ar2).

A number of other taxa from these Great Plains localities are the same species or congeneric with taxa known from the upper Turtle Cove fauna. Along with *Ekgmowechashala*, other taxa known from unit H (Ar1) in the vicinity of Sheep Rock include the following: *Capacikala gradatus*, *Leidymys nematodon*, *Leidymys parvus*, *Nanotragulus planiceps*, *Miohippus annectens*, and *Diceratherium armatum*. Among the most common taxa found in units K1 and K2 (Ar2) in the vicinity of Sheep Rock are *Capacikala gradatus*, *Palaeocastor peninsulatus*, *Pleurolicus sulcifrons*, *Leidymys nematodon*, *Pacaculus insolitus*, and *Promerycochoerus superbus*, as well as *Protosciurus*

mengi, *Nimravus brachyops*, *Mesocyon coryphaeus*, *Nanotragulus planiceps*, *Miohippus annectens*, *Domnina* sp., and *Herpetotherium* sp. The Sharps Fauna localities with *Ekgmowechashala* have also yielded *Capacikala gradatus*, *Palaeocastor peninsulatus*, *Leidymys blacki*, *Leidymys woodi*, *Nanotragulus loomisi*, *Nimravus brachyops*, “*Mesocyon*” *temnodon*, *Miohippus equiceps*, *Diceratherium armatum*, and *Herpetotherium youngi* (Macdonald, 1970; Wang, 1994; Wang et al., 1999; Xu, 1996). In addition to *Ekgmowechashala*, the fauna from the Durnal Ranch Quarry in Nebraska has yielded specimens of *Leidymys blacki*, *Palaeocastor* sp., *Miohippus* cf. *intermedius*, *Domnina dakotensis*, and *Herpetotherium youngi*. The Turtle Butte fauna of South Dakota includes occurrences of *Protosciurus* sp., *Capacikala* sp., *Palaeocastor* sp., *Pleurolicus* sp., *Pacaculus nebraskensis*, and “*Merycochoerus*” *superbus* (Martin, 2011). These faunal similarities support contemporaneous occurrence of *Ekgmowechashala* in the Great Plains and Oregon.

The origin of *Ekgmowechashala*

It is now clear that in the Arikareean, *Ekgmowechashala* appeared simultaneously in Oregon and the Great Plains, but its origin is unknown. *Muangthanhinius siami* from the latest Eocene of Thailand (~34 Ma) and *Bugtilemur mathesoni* from the early Oligocene of Pakistan (~32 Ma) are similar to *Ekgmowechashala* and have recently been placed in the *Ekgmowechashalinae* (Seiffert, 2007). Similarity to these earlier *ekgmowechashalinae* primates from Asia suggests Asian origin for this group and an early or late Oligocene immigration to North America across Beringia (Seiffert, 2007), which was open to dispersal through most of the Paleogene and Neogene (Marincovich and Gladenkov, 1999; Dawson, 2003). Although the simultaneous occurrence of two species of an enigmatic primate taxon of Asian origin 6 million years after the extinction of endemic North American primates may appear problematic, immigration in the late Eocene or early Oligocene would have allowed several million years of time for these late Oligocene species to diverge.

There are some interesting faunal similarities between late Eocene and Oligocene faunas of Asia and Oregon. In addition to *Muangthanhinius*, the latest Eocene Krabi Basin of Thailand has yielded specimens of *Nimravus* cf. *intermedius* and *Hoplophoneus* sp. (Peigné et al. 2000). *Nimravus* is also known from the early Oligocene of Mongolia (de Bonis, 1981; Lange-Badré and Dashzeveg, 1989; Dashzeveg, 1996) and *Nimravus brachyops* is the most common nimravid in the Turtle Cove fauna, ranging from unit C through K1. Several species of *Palaeogale* occur in the early Oligocene of Mongolia; *Palaeogale* sp. is known from units E through H of the Turtle Cove Member in Oregon. Also in Oregon in the early and late Oligocene (Ar1) is a new genus of beaver (Korth and Samuels, In Press) that is very similar to *Propalaeocastor* from the early Oligocene of Europe and Asia, including *P. irtyschensis* from the early Oligocene of China (Wu et al., 2004). These records suggest a number of taxa dispersed between Asia and western North America in the late Eocene or Oligocene.

Paleoecology of *Ekgmowechashala*

The upper and lower molars of *Ekgmowechashala* are characterized by having bulbous cusps with poorly defined crests, including the cristid obliqua, and large

basins. Several studies of primates have found the molars of frugivorous taxa display features that facilitate crushing, including transversely oriented protocristid, buccally located cristid obliqua, and larger talonid basins than faunivorous taxa (Strait, 1993; White, 2009). The weakly developed crests and large basins of *Ekgmowechashala* suggest that crushing, rather than shearing, was the primary function of the teeth and that its diet was primarily frugivorous, as was suggested by Szalay (1976) and Rose and Rensberger (1983). Without more complete cranial and postcranial material, little else can be said regarding the ecology of *Ekgmowechashala*.

Late Eocene and Oligocene paleoenvironments in Oregon

Fossil leaf beds near the Eocene-Oligocene transition have been recognized at many localities across central and eastern Oregon, documenting the ecosystem changes associated with changes toward cooler and more seasonal climates in the early Oligocene (Meyer and Manchester, 1997; Manchester, 2000; Dillhoff et al., 2009). The Bridge Creek Flora assemblage lies near the Eocene-Oligocene boundary itself, dated between 32.99 ± 0.11 Ma and 32.66 ± 0.03 Ma (Retallack et al., 2000). This assemblage documents dramatic floral shifts that coincide with regional and global climate changes, characterized by gradual cooling, increased aridity, and more seasonal precipitation through time (Meyer and Manchester, 1997; Manchester, 2000; Retallack et al., 2000; Retallack, 2004, 2007; Zachos et al., 2001, 2008; Dillhoff et al., 2009).

Paleosol and faunal evidence from the Turtle Cove Member also document significant environmental changes in the Oligocene of Oregon. Through the Arikareean, climate conditions became cooler and drier, woodland habitats began to open up, and bunch grasses and shrubs became more common (Retallack et al., 2000; Retallack, 2004, 2007). This time period includes the appearance of taxa with higher crowned teeth, as well as the region's first appearance of burrowing mammals (palaeocastorine beavers, geomyids, and proscalopids) and cursorial mammals (*Archaeolagus ennisianus*) (Albright et al., 2008; Korth and Samuels, in press). Occurrence of these open habitat adapted taxa with clearly arboreal species, like *Protosciurus* and *Miosciurus*, support reconstruction of Turtle Cove as having a mosaic open woodland environment in the Oligocene. This contrasts strongly with the habitats inhabited by earlier North American primates, specifically relatively warm, closed subtropical forests (Gunnell et al., 2008; Wing, 1998).

The extinction of *Ekgmowechashala* is likely attributable to continued cooling and drying through the late Oligocene. The early late Arikareean (Ar3) aged Kimberly Member overlying Turtle Cove is dominated by open habitat adapted mammals, specifically the entoptychine gopher *Entoptychus* (Rensberger, 1971), and paleosols from these strata suggest much more arid and open environments (Retallack et al., 2000; Retallack, 2007). As the woodland habitats inhabited by *Ekgmowechashala* declined, this last fossil primate in North America vanished with them. Primates were not seen again in North America until the arrival of humans more than 25 million years later.

CONCLUSIONS

The new material of *Ekgmowechashala* described here helps to confirm the presence of this primate in Oregon,

and differences from the previously described *E. philotau* indicate the presence of a distinct new species. Comparison of the known material of *Ekgmowechashala* allows a revised assessment of its relationship to other primates, suggesting placement among the adapiforms. *Ekgmowechashala* and two recently described ekgmowechashaline primates from Asia share a double-rooted p2, molariform p4, mesiodistally compressed molar trigonids, reduced or absent molar paraconids, distinct molar hypoconulids, and crenulated enamel, among other features. Similarity of *Ekgmowechashala* to these two primates from the late Eocene and early Oligocene of Asia suggest ekgmowechashalines originated in Asia and dispersed to North America in the Oligocene, 6 million years after other primates on the continent became extinct. These records also help refine the age range of this primate in North America, which was limited to the early Arikareean (Ar1–Ar2). Combined, the Oregon and Great Plains records indicate the last non-human primates in North America vanished in the late Oligocene, about 26 million years ago.

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