



New occurrences of mammals from McKay Reservoir (Hemphillian, Oregon)

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Non-technical Summary.—The fossil record of the Pacific Northwest records millions of years of changing climate and evolving organisms, shedding light not only on life of the past, but also giving us the tools to better predict how future environmental change might play out. A site near Pendleton, Oregon is especially important to understanding ancient ecosystems because it preserves a complete community of vertebrates, from bats and shrews to rhinos and saber-toothed cats. In 2017 and 2021, we returned to this site to collect new fossils. We also visited museum collections that contain fossils from the site to open as clear a window as possible into this 5–6 million year old world. We identified many species new to the site, many of which are also new to the Northwest. These include a bone-crushing dog; camels, both giant and llama-like; an extinct animal that looked like a deer, but that has no modern relatives; and at least two types of ancient horse. We also compiled a complete, up-to-date list of all the mammals ever found at the site. Besides giving us a better idea of what lived in the Pendleton area in the Miocene Epoch, this work will serve as a jumping-off point for later studies focused on how these organisms behaved, functioned, and interacted with each other and with their environments.

Abstract.—Encompassing global cooling, the spread of grasslands, and biogeographic interchanges, the Hemphillian North American Land Mammal Age is an important interval for understanding the factors driving ecological and evolutionary change through time. McKay Reservoir near Pendleton, Oregon is a natural laboratory for analyses of these factors. It is remarkable for its small vertebrate fauna including rodents, bats, turtles, and lagomorphs, but also for its larger mammal fossils like camelids, rhinocerotids, canids, and felids. Despite the importance of the site, few revisions to its faunal list have been published since its original description. We expand on this description by identifying taxa not previously known from McKay Reservoir based on specimens collected during fieldwork and through reidentification of previously collected fossils. Newly identified taxa include the borophagine canid *Borophagus secundus* (Matthew and Cook, 1909), the camelids *Megatylopus* Matthew and Cook, 1909 and *Pleiolama* Webb and Meachen, 2004, a dromomerycid, and the equids *Cormohipparion* Skinner and MacFadden, 1977 and *Pseudhipparion* Ameghino, 1904. Specimens previously assigned to *Neohipparion* Gidley, 1903 and *Hipparion* de Christol, 1832 lack the features necessary to diagnose these genera, which are therefore removed from the site's faunal list. The presence of *Borophagus secundus*, *Cormohipparion*, and *Pseudhipparion* is especially important, because each occurrence represents a major geographic range extension. This refined understanding of the fauna lays the foundation for future studies of taphonomy, taxonomy, functional morphology, and paleoecology—potentially at the population, community, or ecosystem levels—at this paleobiologically significant Miocene locality.

Introduction

The Hemphillian North American Land Mammal Age (NALMA; Miocene, 9–4.9 Ma; Bell et al., 2004; Tedford et al., 2004; May et al., 2014) spans an interval of profound ecological change, encompassing climatic cooling, the continued spread of grasslands, and the migration of new taxa from Eurasia

and South America (Woodburne, 2004). The McKay Reservoir locality near Pendleton, Oregon (Fig. 1) offers a rare opportunity to study the effects of large-scale change on an ecosystem scale. The site preserves an important Hemphillian-aged vertebrate fauna (Shotwell, 1956). It is especially remarkable for its diversity of small vertebrates, including birds (Brodkorb, 1958), rodents (Martin, 2008), turtles, eulipotyphlans, bats, and lagomorphs (Shotwell, 1956). Larger mammal fossils are also common at the site. The rhinocerotid *Teleoceras* Hatcher, 1894 is particularly abundant (Shotwell, 1956) and the site has also

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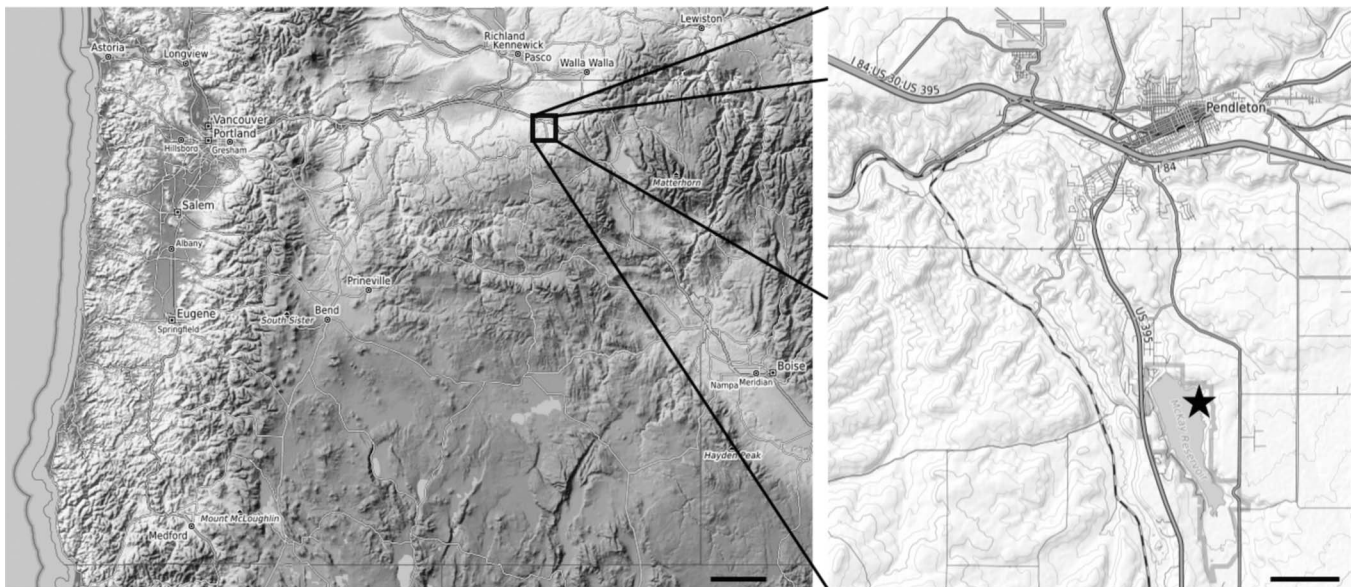


Figure 1. Maps showing location of McKay Reservoir within Oregon (left) and of fossil bearing outcrops along reservoir shoreline (right). Scale bars = 50 km (left); 2 km (right). star, site of fossil bearing outcrops.

yielded a diversity of carnivoran fossils, including borophagine (Wang et al., 1999) and canine canids (Tedford et al., 2009) and the giant felid *Machairodus lahayishupup* Orcutt and Caledo, 2021 (Orcutt and Caledo, 2021). The exceptional completeness of the fossil record from McKay Reservoir has made it a major focus of paleobiological research. Shotwell (1955a) argued that the taphonomy of the McKay Reservoir fossils indicated a pond-bank environment and built on this by including the McKay Reservoir fauna in a pioneering analysis of landscape paleoecology in the Columbia River Basin (Shotwell, 1958). The site's continuing importance as a paleobiological study system is underscored by the many subsequent studies incorporating McKay Reservoir fossils to address questions regarding mammalian body-size evolution (Orcutt and Hopkins, 2013, 2016), morphological variation in mylagaulid rodents (Caledo and Hopkins, 2012), the biogeography of arvicoline rodents (Martin, 2010), the origin of sigmodontine rodents (Ronez et al., 2021), rhinocerotid paleopathology (Stilson et al., 2016), and felid functional morphology and systematics (Orcutt and Caledo, 2021). As extensively and intensely as it has been studied, the McKay Reservoir faunal list continues to grow, due to taxonomic revisions, to previously described taxa, and to new collections made by Gonzaga University field crews in 2017 and 2021. Here, we present the occurrence of several mammalian taxa not previously identified from McKay Reservoir and revisit prior identifications by Shotwell (1956), providing a more complete assessment of diversity in this paleoecosystem and laying the foundation for future paleobiological analyses.

Geologic setting

The McKay Formation, from which the specimens described here were collected, is a component of the late Miocene Dalles Group, previously referred to as the 'Shutler Formation' (Farooqui et al., 1981). The fossil-bearing units of the formation

outcrop only along a 0.3 km section of shoreline on a peninsula on the northeast shore of McKay Reservoir (Fig. 1). The sediments at the locality range from siltstone to conglomerate (Farooqui et al., 1981), with most fossils preserved in the siltstone and sandstone units (Shotwell, 1956). Most McKay Reservoir fossils are found in float along the lake shore, exposed by wave erosion during periods of high water, making it impossible to assign these specimens to a particular stratigraphic unit. As first noted by Shotwell (1956), McKay Reservoir fossils show minimal evidence of abrasion or any other extensive alteration prior to burial. Although some specimens show signs of weathering and breakage, these appear fresh and are likely the result of changing water levels in the reservoir and a strongly seasonal modern climate. However, a detailed taphonomic analysis of the site has not yet been undertaken.

The fossils uncovered from McKay Reservoir are characteristic of the early late Hemphillian (Hh3) NALMA and allow a biochronologic age estimate of 6.7–5.9 Ma (Tedford et al., 2004). Two tephra are interbedded within the fossiliferous layers of the McKay Formation at McKay Reservoir with $^{40}\text{Ar}/^{39}\text{Ar}$ dates of 5.95 ± 0.30 Ma and 5.51 ± 1.22 Ma (Martin et al., 2018). Most fossil sites are between the two tephra but there are rare fossil specimens below the lower ash including possible material of *Megatylopus* Matthew and Cook, 1909. There are abundant fossils in the unit immediately above the upper tephra (Shotwell, 1956; Martin et al., 2018). However, all of these specimens remain consistent with the Hh3 NALMA (Tedford et al., 2004) and therefore are unlikely to significantly pre- or postdate the tephra.

Materials and methods

Many specimens were collected at McKay Reservoir (University of Oregon Locality UO 2222) by field crews from Gonzaga University in July of 2017 and 2021. The reservoir is part of McKay

Creek National Wildlife Refuge and collection was carried out under Permits for Paleontological Investigations issued by the US Bureau of Reclamation (CCAO:U17-001 and CCAO:U21-004) and Special Use Permits issued by the US Fish and Wildlife Service (FF01RMCC00-17-021 and FF01RMCC00-21-005). Measurements of specimens were made to the nearest tenth of a millimeter using Mitutoyo Digital calipers with an accuracy of ± 0.02 mm. In the text and tables, upper dentition is indicated by uppercase letters, lower dentition indicated by lowercase letters.

Repositories and institutional abbreviations.—Specimens from McKay Reservoir are repositied in the following collections: the South Dakota School of Mines and Technology (SDSM; SDSM V for locality numbers), the University of California Museum of Paleontology (UCMP, UCMP V for locality numbers), the University of Oregon Museum of Natural and Cultural History (UOMNH F, UO for locality numbers) and the University of Washington Burke Museum (UWBM VP, UWBM C for locality numbers). Another cited repository is American Museum of Natural History, New York (AMNH).

Systematic paleontology

Order Carnivora Bowdich, 1821
 Family Canidae Fischer De Waldheim, 1817
 Subfamily Borophaginae Simpson, 1945
 Tribe Borophagini Wang et al., 1999
 Subtribe Borophagina Wang et al., 1999
 Genus *Borophagus* Cope, 1892

Type species.—*Borophagus diversidens* Cope, 1892 from the Blancan Blanco Formation at Mt. Blanco, Texas, USA, by original designation.

Borophagus secundus (Matthew and Cook, 1909)
 Figure 2; Table 1

Holotype.—Left ramus (AMNH 13831) from the Hemphillian Johnson Member of the Snake Creek Formation at Sioux County, Nebraska, USA.

Description.—Large size of teeth and presence of small m2 on UOMNH F-81105 and F-81106 suggest that specimens can be



Figure 2. *Borophagus secundus* (Matthew and Cook, 1909) from McKay Reservoir: (1, 2) right dentary (UOMNH F-81105): (1) occlusal view; (2) lateral view; (3) right lower m2 (UOMNH F-81106); (4) left upper M1 in occlusal view (UOMNH F-29746). Scale bar = 1 cm.

Table 1. Measurements of *Borophagus secundus* (Matthew and Cook, 1909) from McKay Reservoir. Anteroposterior (A-P) and mediolateral (M-L) measurements (in mm) shown for upper molars (M), lower premolars (p), and lower molars (m). Mean values for *Borophagus secundus* dental measurements shown in italics (n = 250; Wang et al., 1999). -, not available.

| Specimen | M1 A-P | M1 M-L | p3 A-P | p3 M-L | p4 A-P | p4 M-L | m1 A-P | m1 M-L | m2 A-P | m2 M-L |
|---------------|-------------|-------------|------------|------------|-------------|-------------|-------------|-------------|-------------|------------|
| UOMNH F-29746 | 17.2 | 22.6 | - | - | - | - | - | - | - | - |
| UOMNH F-81105 | - | - | 5.9 | 8.9 | 16.5 | 11.0 | 26.7 | 11.4 | 12.4 | 9.3 |
| UOMNH F-81106 | - | - | - | - | - | - | - | - | 12.7 | 9.3 |
| <i>Mean</i> | <i>16.3</i> | <i>19.6</i> | <i>7.1</i> | <i>8.7</i> | <i>16.1</i> | <i>10.9</i> | <i>26.9</i> | <i>11.3</i> | <i>11.9</i> | <i>8.7</i> |

attributed to a borophagine canid (Wang et al., 1999). Weakly developed mandibular boss below symphysis and smaller width of m1 trigonid than of p4 are all characteristic of *Borophagus* as opposed to *Epicyon* Leidy, 1858. Specimens have several traits characteristic of *Borophagus secundus*: tip of the main cusp of the p4 is higher than the m1 paraconid. P4 is very strongly posteriorly sloped, compressing posterior accessory cusplet; p4 has a triangular shape in occlusal view and overhangs labial face of ramus; roots of p4 are visible on labial side as it is significantly laterally displaced; m1 talonid is reduced; m2 is relatively unreduced; and m2 metaconid is higher than protoconid. Size of UOMNH F-29746 and presence of strong labial cingulum on M1 are consistent with *Borophagus secundus* (Table 1).

Referred material.—UOMNH F-81105, right dentary with p3–m2; UOMNH F-81106, right lower m2; UOMNH F-29746, left upper M1; all specimens from McKay Reservoir (UO 2222).

Remarks.—Although *Borophagus secundus* has been reported from many Hemphillian-aged sites elsewhere in North America, these specimens represent a northward range extension (Wang et al., 1999). Although some fossils described by Shotwell (1963) from the Drewsey Formation of southeaster Oregon could be attributable to *Borophagus secundus*, UOMNH F-81105 marks the first definitive occurrence of the species in Oregon and in the Pacific Northwest more broadly.

Order Artiodactyla Owen, 1848

Family Camelidae Gray, 1821

Tribe Camelini Webb, 1965

Genus *Megatylopus* Matthew and Cook, 1909

Type species.—*Megatylopus gigas* Matthew and Cook, 1909 from the Snake Creek Formation at Nebraska, USA, by original designation.

Megatylopus sp. indet.

Figure 3; Table 2

Description.—Large size (Table 2), relatively low crowns, and lack of cement in fossettes of cheek teeth are characteristic of *Megatylopus* (Jiménez-Hidalgo and Carranza-Castañeda, 2010). Phalanges are intermediate in robusticity (Table 2), as in *Titanotylopus* Barbour and Schultz, 1934, *Megatylopus*, and *Camelops* Leidy, 1854; are consistent in size with *Megatylopus* and *Camelops*; and have a W-shaped suspensory ligament scar, as in *Titanotylopus* and *Megatylopus* (Voorhies and Corner, 1986).

Referred material.—SDSM 12812, proximal phalanx; SDSM 15826, proximal phalanx; SDSM 28013, proximal phalanx; SDSM 51260, right M3; UCMP 113536, proximal phalanx; UOMNH F-3843, proximal phalanx; UOMNH F-4152, proximal phalanx; UOMNH F-4153, proximal phalanx; UOMNH F-71508, proximal phalanx; UOMNH F-81109, left M1 or M2; UOMNH F-81110, proximal phalanx; UOMNH F-81111, proximal phalanx; UWBM VP 61682, left m1 or m2; all specimens from McKay Reservoir (SDSM V802, UCMP V74163, UO 2222, UWBM C0128).

Remarks.—Shotwell (1956) indicated the presence of a large and small camelid at McKay Reservoir but did not identify these camelids to genus. The larger material described above is referable to *Megatylopus*, the first definitive identification of this genus at McKay Reservoir, although Martin et al. (2010) indicated the presence of the genus at the site without assigning specific specimens to it. Many of the specimens are smaller than those found at sites elsewhere in North America (Table 2; Voorhies and Corner, 1986; Jiménez-Hidalgo and Carranza-Castañeda, 2010) although UOMNH F-4152 is extremely large, indicating a wide range of body sizes (Table 2). Whether this is the result of sexual dimorphism, the presence of multiple species, or simply normal variation within *Megatylopus* cannot be ascertained based on the sample size currently available.

Tribe Lamini Webb, 1965

Genus *Pleiolama* Webb and Meachen, 2004

Type species.—*Pleiolama mckennai* Webb and Meachen, 2004 from the Clarendonian Merritt Dam Member of the Ash Hollow Formation at Kat Quarry, Nebraska, USA, by original designation.

Pleiolama sp. indet.

Figure 4; Table 2

Description.—Small size of molar is consistent with *Pleiolama*, particularly with the small species *Pleiolama vera* (Matthew, 1909); although *Pleiolama* and *Alforjas* Harrison, 1979 are similar in size, lower degree of hypsodonty is consistent with *Pleiolama* (Webb and Meachen, 2004). Elongated, gracile phalanx indicates that UOMNH F-4154 and UOMNH F-81112 are referable to Lamini (Harrison, 1979). Presence of W-shaped suspensory ligament scar that does not extend far down the phalangeal shaft indicates that the specimens can be referred to the lamins *Alforjas* or *Hemiauchenia* Gervais and Ameghino, 1880 (sensu Harrison, 1979, equivalent to

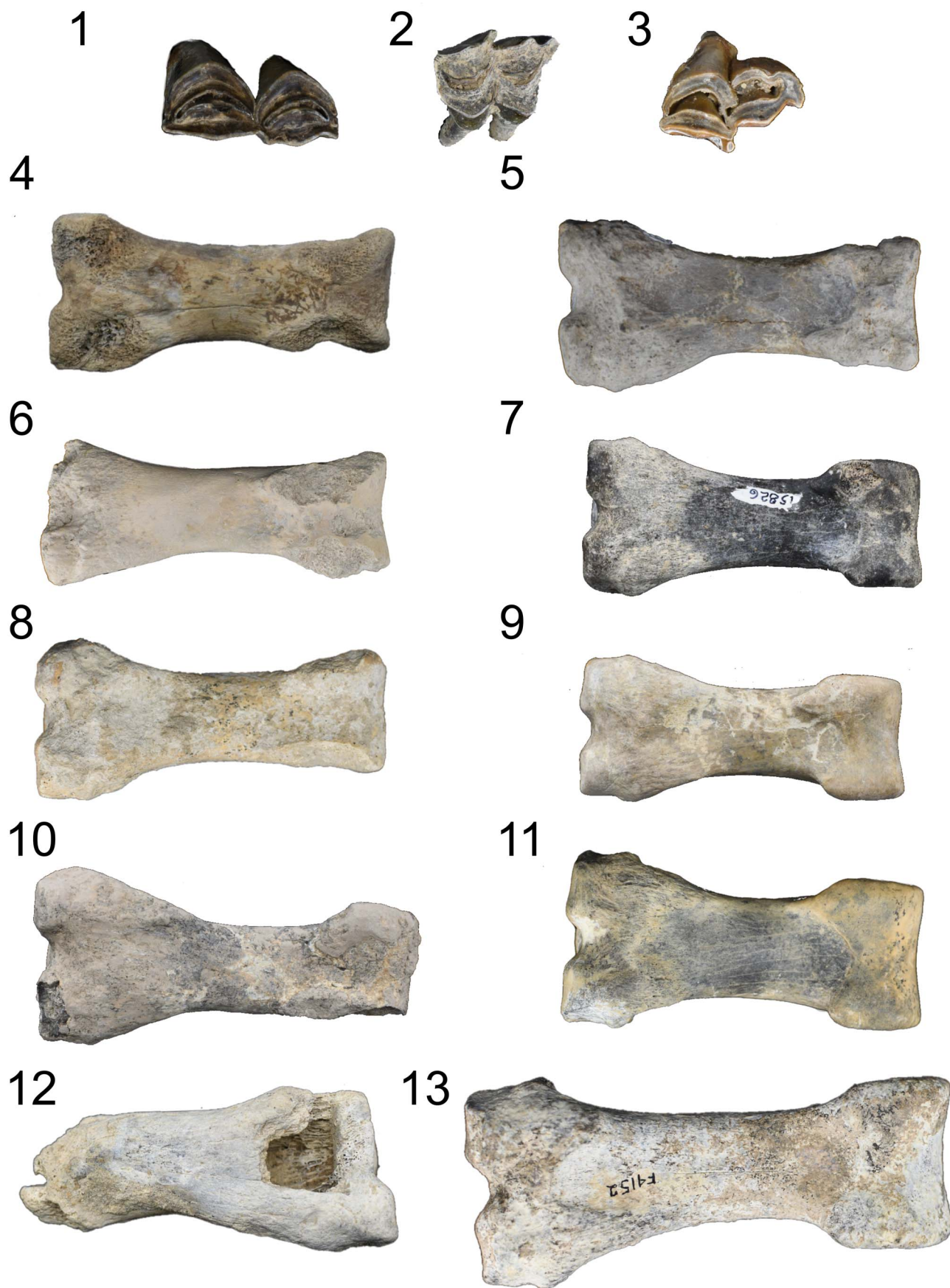


Figure 3. *Megatylopus* sp. indet. from McKay Reservoir: (1) left m1 or m2 in occlusal view (UWBM 61682); (2) left M1 or M2 in occlusal view (UOMNH F-81109); (3) right M3 (SDSM 51260); (4–13) proximal phalanges in plantar view: (4) UOMNH F-81111; (5) UOMNH F-81110; (6) UCMP 113536; (7) SDSM 15826; (8) UOMNH F-4153; (9) SDSM 28013; (10) SDSM 12812; (11) UMNH F-3843; (12) UOMNH F-71508; (13) UOMNH F-4152. Scale bar = 1 cm.

Table 2. Measurements of artiodactyls from McKay Reservoir. Mediobasilar (M-L) measurements (in mm) shown for upper molars (M), lower molars (m), and proximal phalanges. Length measured anteroposteriorly (A-P) for molars and proximodistally (P-D) for phalanges. Mediobasilar measurements of phalanges made at the proximal end of the bone. Mean values for the upper molars from the species description of multiple camelid and dromomerycid species shown in italics, including *Megatylopus gigas* Matthew and Cook, 1909 (n = 1), *Megatylopus cochrani* (Hibbard and Riggs, 1949) (n = 1), *Megatylopus matthewi* Webb, 1965 (n = 2), *Megatylopus primaevus* Patton, 1969 (n = 1), *Pleiolama mckennai* Webb and Meachen, 2004 (n = 5), and *Yumaceras hamiltoni* (Webb, 1983) (n = 5 M3, 10 M, 16 m).

| Taxon | Specimen | M3 A-P | M3 M-L | M A-P | M M-L | m A-P | m M-L | phalanx P-D | phalanx M-L |
|--------------------|---------------------|--------|--------|-------|-------|-------|-------|-------------|-------------|
| <i>Megatylopus</i> | SDSM 12812 | - | - | - | - | - | - | 110.6 | 48.1 |
| | SDSM 15826 | - | - | - | - | - | - | 95.9 | 42.2 |
| | SDSM 28013 | - | - | - | - | - | - | 95.6 | 40.4 |
| | SDSM 51260 | 39.4 | 23.5 | - | - | - | - | - | - |
| | UCMP 113536 | - | - | - | - | - | - | 103.9 | 36.2 |
| | UOMNH F-3843 | - | - | - | - | - | - | 102.5 | 50.9 |
| | UOMNH F-4152 | - | - | - | - | - | - | 136.4 | 58.5 |
| | UOMNH F-4153 | - | - | - | - | - | - | 102.6 | 45.9 |
| | UOMNH F-71508 | - | - | - | - | - | - | 107.3 | 45.4 |
| | UOMNH F-81109 | - | - | 40.1 | 26.0 | - | - | - | - |
| | UOMNH F-81110 | - | - | - | - | - | - | 99.9 | 44.9 |
| | UOMNH F-81111 | - | - | - | - | - | - | 101.5 | 46.1 |
| | UWBM VP 61682 | - | - | - | - | 49.2 | 24.1 | - | - |
| | <i>M. gigas</i> | - | - | 33.0 | 39.4 | 45.0 | 41.0 | 128.0 | 52.0 |
| | <i>M. cochrani</i> | - | - | - | - | - | - | 127.0 | - |
| | <i>M. matthewi</i> | 56.3 | 21.5 | 35.5 | 22.8 | - | - | - | - |
| | <i>M. primaevus</i> | - | - | - | - | 38.5 | 19.9 | - | - |
| <i>Pleiolama</i> | SDSM 59835 | - | - | - | - | 20.5 | 9.4 | - | - |
| | UOMNH F-4154 | - | - | - | - | - | - | 79.2 | 26.9 |
| | UOMNH F-81112 | - | - | - | - | - | - | 89.1 | 25.9 |
| Dromomerycidae | <i>P. mckennai</i> | 28.4 | 17.8 | 25.3 | 18.9 | 25.4 | 16.2 | - | - |
| | SDSM 38459 | - | - | 16.5 | 13.8 | - | - | - | - |
| | <i>Y. hamiltoni</i> | 22.6 | 23.2 | 21.7 | 22.6 | 21.6 | 15.6 | - | - |

Pleiolama; Webb and Meachen, 2004). Relatively narrow proximal end of phalanx is inconsistent with *Alforjas* (Table 2).

Referred material.—SDSM 59835, right m1 or m2; UOMNH F-4154, proximal phalanx; UOMNH F-81112, proximal phalanx; both from McKay Reservoir (SDSM V802, UO 2222).

Remarks.—The small camelid described by Shotwell (1956) is referable to *Pleiolama*. Although lamins, including *Pleiolama*, are known from regional Hemphillian-aged sites in Oregon’s Rattlesnake Formation (Fremd, 2010) and Washington’s Ellensburg Formation (Martin and Pagnac, 2009), this is the first identification of the genus from McKay Reservoir.

Family Dromomerycidae Frick, 1937
 Dromomerycidae gen. indet. sp. indet.
 Figure 5; Table 2

Description.—Relatively small selenodont and brachydont molar that is consistent with both Cervidae and Dromomerycidae. However, the lack of complex folding on the protoconal and metaconule crests is inconsistent with *Bretzia* Fry and Gustafson, 1974 and other cervids (Gustafson, 2015). Of the two unequivocally Hemphillian-aged dromomerycid genera (Frick, 1937; Janis and Manning, 1998), the brachydonty of the McKay Reservoir specimen is consistent with *Yumaceras* Frick, 1937, but the small size of the tooth might be more consistent with *Pediomeryx* Stirton, 1936 (Table 2; Prothero and Leiter, 2008).

Referred material.—SDSM 38459, left M1 or M2, from McKay Reservoir (SDSM V802).

Remarks.—Isolated upper molars such as SDSM 38459 are generally not diagnostic for dromomerycids, in which lower

dentition and ossicones are of predominant importance. *Pediomeryx* is the most common and widespread dromomerycid of the late Hemphillian, but SDSM 38459 bears a stronger resemblance to *Yumaceras* in its brachydonty (Prothero and Lister, 2008). However, its size falls well below the range reported by Webb (1983) in his description of *Yumaceras hamiltoni* (Table 2). *Pediomeryx hemphillensis* is smaller in size than *Yumaceras hamiltoni* (Webb, 1983; Prothero and Lister, 2008), but a paucity of published measurements of upper dentition for this species hinders quantitative comparisons. If SDSM 38459 does represent *Yumaceras*, its occurrence at McKay Reservoir would be a slight range extension; it has previously only been reported in the Pacific Northwest from the earlier Hemphillian-aged Drewsey Formation of southeastern Oregon (Prothero and Lister, 2008). *Pediomeryx* has not previously been reported from the region.

Order Perissodactyla Owen, 1848
 Family Equidae Gray, 1821
 Subfamily Equinae Steinmann and Döderlein, 1890
 Equinae gen. indet. sp. indet.
 Figure 6.7; Table 3

Referred material.—UOMNH F-4444, buccal half of an upper cheek tooth other than P2 or M3, from McKay Reservoir (UO 2222).

Remarks.—UOMNH F-4444 is the only specimen in any collection that we could find that was identified in collections as *Neohipparion*. Shotwell (1955a, 1956, 1958) reported one occurrence of *Neohipparion* but never identified the specimen. This specimen is broken so that the lingual half is missing, thus removing any of the diagnostic characteristics for any more specific identification. As such, we are



Figure 4. *Pleiolama* sp. indet. from McKay Reservoir: (1, 2) right m1 or m2 (SDSM 59835): (1) occlusal view; (2) lateral view; (3, 4) proximal phalanges in plantar view: (3) UOMNH F-81112; (4) UOMNH F-4154. Scale bar = 1 cm.

removing the occurrence of *Neohipparion* from the faunal list for McKay Reservoir.

Tribe Hipparionini Quinn, 1955

Genus *Cormohipparion* Skinner and MacFadden, 1977

Type species.—*Cormohipparion* (= *Hipparion*) *occidentale* (Leidy, 1856) from the Neogene at Little White River, South Dakota, USA, by original designation.

Cormohipparion sp. indet.

Figure 6.1–6.5; Table 3

Description.—Large teeth (Table 3). Protocone small and isolated; complex plications on the pre- and post-fossettes; well-developed pli caballins. More specific identification is difficult with isolated teeth because they lack a majority of diagnostic characters (Famoso and Davis, 2014).

Referred material.—UOMNH F-2763, right maxilla fragment with P2–P4; UOMNH F-2787, left upper cheek tooth other than P2 or M3; UOMNH F-4156, left upper cheek tooth fragment; UWBM VP 61573, left P2; UWBM VP 61653, left maxilla fragment with P2 – P3; all from McKay Reservoir (UO 2222, UWBM C0128).

Remarks.—UOMNH F-2763, F-2757, F- 4156, and UWBM VP 61653 and VP 61573 mark the first definitive occurrences of *Cormohipparion* in Oregon. It is likely that specimens identified as *Hipparion* by Shotwell (1955a, 1956, 1958) are *Cormohipparion*, because he never identified the specific specimens that he assigned to *Hipparion*. Additionally, Skinner and MacFadden (1977) named *Cormohipparion* from material previously identified as *Hipparion* in North America well after Shotwell’s original work. We have reviewed all of the relevant specimens and have not found any that meet the diagnosis for *Hipparion* and suggest removing it from the faunal list and replacing it with *Cormohipparion*. Measurements of these referred specimens are not consistent



Figure 5. Dromomerycidae gen. indet. sp. indet. from McKay Reservoir, left M1 or M2 (SDSM 38459): (1) occlusal view; (2) medial view; (3) lateral view. Scale bar = 1 cm.



Figure 6. Equids from McKay Reservoir: (1–5) *Cormohipparion* sp. indet., upper dentition: (1) left maxilla fragment with P2–P3 in occlusal view (UWBM VP 61653); (2) right maxilla fragment with P2–P4 in occlusal view (UOMNH F-2763); (3) left upper cheek tooth other than P2 or M3 in occlusal view (UOMNH F-2787); (4) left upper cheek tooth other than P2 or M3 in occlusal view (UWBM VP 61573); (5) left upper cheek tooth fragment in occlusal view (UOMNH F-4156); (6) *Pseudhipparion* sp. indet., right upper cheek tooth other than P2 or M3 in occlusal view (UOMNH F-29959); (7) Equinae gen. indet. sp. indet., buccal half of upper cheek tooth other than P2 or M3 in occlusal view previously assigned to *Neohipparion* (UOMNH F-4444). Scale bar = 1 cm.

with the species means of previously described species (Table 3). Furthermore, for specimens with multiple teeth, the most similar species varied with tooth position. UOMNH F-2787 is most comparable in size to *Cormohipparion skinneri* but is still fairly far off. The dimensions of

UOMNH F-2763, and UWBM VP 61573 and VP 61653 are not consistent with those of any other species of *Cormohipparion*. Because the numerical data are not conclusive and there are no qualitative characteristics on each of these teeth that can definitively place these specimens into a

Table 3. Measurements of equids from McKay Reservoir. Anteroposterior (A-P) and mediolateral (M-L) measurements (in mm) are shown for upper premolars (P), upper molars (M), and upper cheek teeth (CT). Due to its fragmentary nature, measurements of UOMNH F-4156 (*Cormohipparion* sp. indet.) are not included. Mean values for the upper molars from the species description of multiple *Cormohipparion* and *Pseudhipparion* species are shown in italics, including *Cormohipparion occidentale* (Leidy, 1856) (n = 1), *Cormohipparion emsliei* Hulbert, 1988 (n = 5 P2, 24 M), *Cormohipparion fricki* Woodburne, 2007 (n = 6), *Cormohipparion goorisi* MacFadden and Skinner, 1981 (n = 4), *Cormohipparion johnsoni* Woodburne, 2007 (n = 2), *Cormohipparion matthewi* Woodburne, 2007 (n = 4), *Cormohipparion merriami* Woodburne, 2007 (n = 4), *Cormohipparion plicatile* (Leidy, 1887) (n = 1), *Cormohipparion quinni* Woodburne, 1996 (n = 14), *Cormohipparion skinneri* Woodburne, 2007 (n = 2), *Cormohipparion sphenodus* (Cope, 1889) (n = 2), *Pseudhipparion retrusum* (Cope, 1889) (n = 2), *Pseudhipparion gratum* (Leidy, 1869) (n = 2), *Pseudhipparion hessei* Webb and Hulbert, 1986 (n = 43 P2, 24 M), *Pseudhipparion simpsoni* Webb and Hulbert, 1986 (n = 5 P2, 24 M), and *Pseudhipparion skinneri* Webb and Hulbert, 1986 (n = 11 P2, 44 M). -, not available.

| Taxon | Specimen | P2 A-P | P2 M-L | P3 A-P | P3 M-L | P4 A-P | P4 M-L | M A-P | M M-L | CT A-P | CT M-L |
|-----------------------|-----------------------|--------|--------|--------|--------|--------|--------|-------|-------|--------|--------|
| Equinae | UOMNH F-4444 | - | - | - | - | - | - | - | - | 21.1 | - |
| <i>Cormohipparion</i> | UOMNH F-2763 | - | 28.5 | 27.8 | 22.0 | 26.2 | 17.5 | - | - | - | - |
| | UOMNH F-2787 | - | - | - | - | - | - | - | - | 28.7 | 28.0 |
| | UWBM VP 61573 | 29.1 | 24.0 | - | - | - | - | - | - | - | - |
| | UWBM VP 61653 | 26.2 | 23.2 | 29.0 | 22.0 | - | - | - | - | - | - |
| | <i>C. occidentale</i> | 31.8 | 22.2 | - | - | - | - | 25.4 | 24.3 | - | - |
| | <i>C. emsliei</i> | 23.7 | 18.1 | - | - | - | - | 19.2 | 17.2 | - | - |
| | <i>C. fricki</i> | 30.4 | 23.2 | 26.4 | 25.5 | 25.5 | 25.5 | 23.3 | 23.0 | - | - |
| | <i>C. goorisi</i> | 22.7 | 19.4 | 19.9 | 21.4 | 19.5 | 21.5 | 17.7 | 20.9 | - | - |
| | <i>C. johnsoni</i> | 27.6 | 21.0 | 24.4 | 23.3 | 23.6 | 23.9 | 21.7 | 22.3 | - | - |
| | <i>C. matthewi</i> | 28.5 | 21.7 | 24.6 | 23.6 | 22.9 | 22.9 | 21.5 | 20.0 | - | - |
| | <i>C. merriami</i> | 30.6 | 23.6 | 26.3 | 25.7 | 24.4 | 25.3 | 22.0 | 23.2 | - | - |
| | <i>C. plicatile</i> | - | - | - | - | - | - | 20.0 | 23.0 | - | - |
| | <i>C. quinni</i> | 25.7 | 20.2 | 22.4 | 23.2 | 24.4 | 22.3 | 20.1 | 21.1 | - | - |
| | <i>C. skinneri</i> | 33.3 | 25.2 | 28.4 | 27.4 | 27.0 | 26.8 | 24.7 | 25.5 | - | - |
| | <i>C. sphenodus</i> | 25.0 | 28.0 | 25.0 | 18.0 | - | - | 22.0 | 17.0 | - | - |
| <i>Pseudhipparion</i> | UOMNH F-29959 | - | - | - | - | - | - | 15.9 | 14.7 | - | - |
| | <i>P. retrusum</i> | - | - | - | - | - | - | 19.5 | 18.3 | - | - |
| | <i>P. gratum</i> | 10.5 | 8.5 | - | - | - | - | 16.9 | 16.9 | - | - |
| | <i>P. hessei</i> | 20.9 | 16.2 | - | - | - | - | 16.9 | 16.5 | - | - |
| | <i>P. simpsoni</i> | 13.0 | 11.5 | - | - | - | - | 12.6 | 12.3 | - | - |
| | <i>P. skinneri</i> | 18.3 | 14.1 | - | - | - | - | 14.3 | 13.7 | - | - |

Table 4. Updated faunal list for McKay Reservoir. Taxa first described by Shotwell (1956, 1958, 1967a, b) in his initial work on the locality, by subsequent authors (Lindsay, 1962; Hutchison, 1968; Wagner, 1976; Harrison, 1981; Martin, 1984, 1998; Korth, 1999; Prothero, 2005; Orcutt and Calede, 2021), and in this paper are shown. X, the original taxonomic assignment is still valid; O, taxonomy has been updated since its original description; ?, taxonomic assignment uncertain; -, not applicable.

| Taxon | J.A. Shotwell | Subsequent Authors | This Paper |
|---|---------------|--------------------|------------|
| Eulipotyphla | | | |
| <i>Scapanus</i> cf. <i>S. proceridens</i> Hutchinson, 1968 | O | X | - |
| <i>Gaillardia thomsoni</i> Matthew, 1932 | O | X | - |
| <i>Scalopoides</i> sp. indet. | - | ? | - |
| <i>Yanshuella columbiana</i> (Hutchinson, 1968) | - | X | - |
| Chiroptera | | | |
| Chiroptera indet. | X | - | - |
| Lagomorpha | | | |
| <i>Ochotona spangle</i> Shotwell, 1956 | X | - | - |
| <i>Hypolaqus oregonensis</i> Shotwell, 1956 | X | - | - |
| Rodentia | | | |
| <i>Liodontia</i> sp. indet. | X | - | - |
| <i>Hesperogaulus wilsoni</i> Korth, 1999 | O | X | - |
| <i>Parapaenemarmota oregonensis</i> (Shotwell, 1956) | O | X | - |
| <i>Otospermophilus wilsoni</i> (Shotwell, 1956) | X | - | - |
| <i>Spermophilus mckayensis</i> (Shotwell, 1956) | X | - | - |
| <i>Neotamias</i> sp. indet. | - | X | - |
| <i>Parapliosacomys oregonensis</i> Shotwell, 1967a | X | - | - |
| <i>Oregonomys sargenti</i> (Shotwell, 1956) | O | X | - |
| Perognathinae gen. indet. sp. indet. | - | X | - |
| Dipodomysinae gen. indet. sp. indet. | - | X | - |
| <i>Leptodontomys oregonensis</i> Hibbard, 1970 | X | - | - |
| <i>Dipoides smithi</i> Shotwell, 1955b | X | - | - |
| <i>Castor</i> sp. indet. | X | - | - |
| <i>Peromyscus mimus</i> Shotwell, 1956 | X | - | - |
| <i>Peromyscus antiquus</i> Kellogg, 1910 | X | - | - |
| <i>Postcopemys</i> cf. <i>P. valencis</i> (Shotwell, 1967b) | O | X | - |
| <i>Basirepomys pliocenicus</i> (Wilson, 1937) | O | X | - |
| <i>Copemys esmeraldensis</i> Clark, Dawson, and Wood, 1964 | - | X | - |
| <i>Pliozapus solus</i> Wilson, 1936 | X | - | - |
| Carnivora | | | |
| <i>Eucyon davisi</i> (Merriam, 1911) | O | X | - |
| <i>Borophagus secundus</i> (Matthew and Cook, 1909) | O | - | X |
| <i>Plesiogulo marshalli</i> (Martin, 1928) | O | X | - |
| <i>Mustela</i> sp. indet. | X | - | - |
| <i>Pliotaxidea nevadensis</i> (Butterworth, 1916) | O | X | - |
| <i>Lynx longignathus</i> (Shotwell, 1956) | O | X | - |
| <i>Machairodus lahayishup</i> Orcutt and Calede, 2021 | O | X | - |
| Proboscidea | | | |
| Mammutidae gen. indet. sp. indet. | ? | - | - |
| Perissodactyla | | | |
| <i>Cormohipparion</i> sp. indet. | O | - | X |
| <i>Hipparion</i> sp. indet. | O | - | - |
| <i>Neohipparion</i> sp. indet. | ? | - | - |
| <i>Pseudhipparion</i> sp. indet. | - | - | X |
| <i>Teleoceras hicksi</i> Cook, 1927 | O | X | - |
| Artiodactyla | | | |
| <i>Platygonus brachirostris</i> (Shotwell, 1956) | O | X | - |
| <i>Pleiolama</i> sp. indet. | O | - | X |
| <i>Megatylopus</i> sp. indet. | O | - | X |
| Palaeomerycidae gen. indet. sp. indet. | - | - | X |

specific species, we leave these specimens identified to the level of genus.

Genus *Pseudhipparion* Ameghino, 1904

Type species.—*Pseudhipparion* (= *Hipparion*) *retrusum* (Cope, 1889) from the Neogene Ogallala Formation at Phillips County, Kansas, USA, by original designation.

Pseudhipparion sp. indet.

Figure 6.6; Table 3

Description.—Small tooth (Table 3). Protocone large, elliptical, and isolated in early wear stages but appears to connect in later wear stages (estimated from observance on the exterior of the

tooth); simple plications on both fossettes; prominent hypoconal lake. More specific identification is difficult with isolated teeth because they lack a majority of diagnostic characters (Famoso and Davis, 2014).

Referred material.—UOMNH F-29959, right upper cheek tooth other than P2 or M3, from McKay Reservoir (UO 2222).

Remarks.—UOMNH F-29959 marks the first published occurrence of the genus in Oregon and the Pacific Northwest, as well as west of the Rocky Mountains. When the length and width of the specimen are compared to mean values for previously described species (Table 3), this tooth is not consistent with *Pseudhipparion skinneri* Webb and Hulbert,

1986, *Pseudhipparion gratum* (Leidy, 1869), or *Pseudhipparion hessei* Webb and Hulbert, 1986. There are no other qualitative or quantitative diagnostic features on this tooth that can be used to differentiate among the three species, therefore we leave the specimen identified to the genus level.

Discussion

Besides adding to the McKay Reservoir faunal list, the specimens described above underscore the paleobiological significance of the site. Most importantly, these occurrences mark major geographic range extensions for three taxa (*Borophagus secundus*, *Pseudhipparion* sp. indet., and *Cormohipparion* sp. indet.), none of which had been definitively identified in Oregon and of which only *Cormohipparion* had previously been described from any sites in the Pacific Northwest (Rapp, 2006). Their presence at McKay Reservoir reflects the remarkable completeness of the paleocommunity and further solidifies the value of the site as a natural laboratory for Hemphillian paleoecology, a point that is illustrated by comparison with other geographically constrained Hemphillian-aged formations in the Pacific Northwest. Following this analysis, 40 mammalian taxa have been reported from McKay Reservoir (Table 4). By contrast, the Rattlesnake Formation of the John Day Basin has yielded 29 described mammalian taxa and the Thousand Creek Formation of northern Nevada has yielded 30 (https://paleobiodb.org/data1.2/occs/list.csv?datainfo&rowcount&base_name=Mammalia&strat=Thousand Creek, Rattlesnake, downloaded from the Paleobiology Database on 3 October 2023). Expanding these comparisons beyond the Pacific Northwest, McKay Reservoir's mammalian diversity is comparable to one of the sites from Texas' Hemphill Beds for which the Hemphillian is named (Coffee Ranch, 45 taxa) and surpasses the other (Higgins Quarry, 30 taxa; https://paleobiodb.org/data1.2/occs/list.csv?datainfo&rowcount&base_name=Mammalia&interval=Hemphillian,Hemphillian&cc=US&state=Texas&county=Hemphill, Lipscomb, downloaded from the Paleobiology Database on 28 November 2023). Having better established the composition and completeness of the mammal fauna, a logical next step along with continuing field work would be reconstructing interactions between the members of that fauna through stable isotope analysis of mammal teeth. Fossils from the site could also inform broader quantitative taxonomic analyses of taxa such as *Megatylopus*, *Cormohipparion*, and *Pseudhipparion*, possibly allowing the identification of existing specimens to the species level.

The McKay paleocommunity consists of not only mammals but fish, amphibians, and an abundance of reptiles and birds, most of which have not been a focus of study since the original descriptions by Shotwell (1956) and Brodkorb (1958). Note that, among the comparable regional formations mentioned above, the only description of any nonmammalian taxon is the turtle *Clemmys hesperia* Gray, 1825 from the Rattlesnake Formation (Hay, 1903). Given the importance of these taxa as environmental indicators, a revision of the ichthyofauna, herpetofauna, and avifauna of McKay Reservoir and other Dalles Group localities will provide a more complete paleoecological context. A clearer understanding of the physical environment of the McKay paleoecosystem is also crucial, particularly

because Shotwell's (1955a) interpretation of the site as a pond-bank community is not consistent with the coarser-grained lithology of the bluff from which the fossils weather (Martin et al., 2018). Along with sedimentology, stratigraphy, and paleopedology, ichnology could also provide valuable information about the McKay paleoenvironment, because burrows consistent in size with those of fossorial rodents were visible in some of the lower units of the McKay Formation. Establishing as clear as possible an environmental context would make it possible to undertake analyses not feasible in many paleoecosystems, e.g., reconstructing food webs or population-level morphological patterns in well-represented taxa including rhinocerotids, sciurids, and camelids. Additional fieldwork and the review of previously collected material is pivotal to our understanding of the McKay Formation and the Hemphillian of the Pacific Northwest, revealing a more complete picture of the fauna, providing increased sample sizes for paleobiological analyses, and allowing comparisons with coeval localities across North America.

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Declaration of competing interests

The authors declare none.

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