ABSTRACT—The Hemingfordian North American Land Mammal Age is not well sampled, especially in the Pacific Northwest. Here we present both a description of a new fauna and two radiometric dates, 16.26 Ma and 16.44 Ma, constraining the Hawk Rim locality of central Oregon. Hawk Rim represents the first diverse late Hemingfordian fauna in the Northwest and is one of the stratigraphically lowest fossiliferous outcrops of the Mascall Formation. Much of Oregon was blanketed by Columbia River Flood Basalts during late Hemingfordian time, limiting not only outcrops but places for organisms to have survived. The site yields a taxonomically rich fauna sharing strong faunal similarity with the type locality of the Mascall but also containing taxa new to the formation and region. We describe occurrences of five genera of Artiodactyla, four genera of Perissodactyla, three genera of Rodentia, and six genera of Carnivora, with all but three new occurrences for the Hemingfordian of the Pacific Northwest. In particular, the carnivore fauna extends the geographic and temporal range of several carnivorans, and we describe a new hypercarnivorous mustelid, Watay tabutsigwii.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

INTRODUCTION

Although the Pacific Northwest has an excellent fossil record of terrestrial mammals through most of the Cenozoic, few localities yield faunas from the Hemingfordian North American Land Mammal Age (NALMA; Tedford et al., 2004). The John Day Formation includes sparse early Hemingfordian faunas (Albright et al., 2008), but there are no known terrestrial vertebrate faunas from the middle or late Hemingfordian of Oregon or Washington. The Massacre Lake fauna near Virgin Valley, Nevada, is the nearest record of the latest Hemingfordian, representing one of the few sites in the intermontane west to preserve the late Hemingfordian time period. However, although radiometric dating places the fossils from this locality around 16.47 Ma (Morea, 1981), this is likely an overestimate in age, because it is an older argon date. The fauna is, furthermore, not entirely constrained by the single date and shares more of the fauna in common with Barstovian localities than Hawk Rim.

The Middle Miocene, with global warming followed by a cooling climate (Zachos et al., 2008), set the stage for the continued expansion of open habitats and the resulting faunal turnover in the western United States. As grasslands reshaped the landscape, replacing the previous vegetation (Jacobs et al., 1999; Edwards et al., 2010), new faunas migrated or evolved to exploit the changing resources. Yet the ecology of terrestrial habitats, especially in the intermontane west, was far from a simple linear progression from one biome to another (Retallack, 2004). The Hawk Rim fauna typifies how ecological heterogeneity shaped the diverse faunas of the region and showcases the transition into the drier and cooler type locality Mascall fauna.

Hawk Rim is a newly discovered late Hemingfordian site in central Oregon. This locality fills both temporal and geographic gaps between other localities (Fig. 1). It was discovered in 2008 through a collaborative effort between the Park Service and the Bureau of Land Management. Both regional proximity and, most importantly, lithologic and stratigraphic similarities suggest its inclusion in the Mascall Formation.

Oregon possesses a relatively complete Miocene fossil record, and Hawk Rim, in particular, presents an ideal location to add to our understanding of the Middle Miocene, filling existing gaps in spatial and temporal coverage. Stratigraphically lower and older than the more well-known type locality of the Mascall Formation, Hawk Rim extends the geographic and temporal extent of the fossiliferous portion of the formation. The Mascall fauna is among those included in Oregon’s John Day Fossil Beds National Monument. This extensive formation has yielded fossils to paleontologists for well over 150 years. Horses from the Mascall collected by Thomas Condon were used by Marsh to support the then-controversial theory of evolution (Drake, 1978). Little work has occurred in the last 50 years, while the understanding of both the fossils and the geology expanded. Regional faunas of similar ages include the Simtustus Formation to the west of main outcrops of the Mascall Formation (Smith, 1986), eastern Sucker Creek Formation (Downing, 1992), southern Virgin Valley Formation faunas (Wendell, 1970), and Deer...
Butte Formation and the fauna of the Butte Creek Volcanic Sandstone to the east and south (Shotwell, 1968). These formations span the early Hemingfordian to the late Barstovian North American Land Mammal Age (NALMA; Tedford et al., 2004). Identification of key biostratigraphic marker taxa allows for assignment to individual NALMAs or even subsections of NALMAs. Hawk Rim serves to fill a gap between the Pacific Northwest’s diverse and well-sampled (but very different in ecology and fauna) Arikareean and Barstovian, and although the Hawk Rim fauna shares similarities with the Northwest’s Barstovian faunas, it also contains faunal similarities to the very different faunas of the Barstovian of the Great Plains.

Hawk Rim lies west and south of the type locality of the Mascall Formation, which is primarily observed in the John Day Valley of eastern Oregon (Walker and MacLeod, 1991). To the northwest is the Simtustus Formation, also of Barstovian age, outcropping on and around the Warm Springs Indian Reservation. To the southeast, the Owyhee region contains excellent faunas from the early Barstovian, including the Red Basin and Quartz Basin faunas. Both of these faunas sample the early Barstovian and are likely representative of both the ecological and biological diversity occurring in the region with their markedly different faunal compositions (Shotwell, 1968; Janis et al., 1998).

Farther south, the Sucker Creek Formation also yields a fauna of early Barstovian age (Downing, 1992). Although outside of Oregon, the Massacre Lake and Virgin Valley faunas of northern Nevada, near the southeast corner of Oregon, contain fauna from the latest Hemingfordian and early Barstovian, respectively (Morea, 1981; Wendell, 1970). Late Hemingfordian sites are more limited (Woodburne et al., 2004). Lying on the central western edge of the distribution of northwest sites, Hawk Rim adds increased ecological diversity and a more complete sampling of the Hemingfordian-Barstovian boundary. Sampling a slightly earlier time period than the far more common Barstovian sites, Hawk Rim’s fauna shares many taxa in common with the regional early Barstovian faunas, yet adds several taxa previously unknown from the Pacific Northwest and exhibits species abundances different from those observed in many mid-Miocene sites in the region (Table 1).
forests found in the Upper Mascall Formation (Chaney and Axelrod, 1959; Bestland, 1998).

METHODS

Geology

Outcrops at Hawk Rim were located through surface surveys, aerial photography, and consultation with John Zancanella of the Bureau of Land Management Prineville District. Preliminary investigations occurred over one day of field investigations in 2008, conducted by staff from the John Day Fossil Beds National Monument. Limited material was collected, including a Tephrocyon rasuretis tooth and astragali and teeth from Merychippus, Archaeohippus, and Desmatippus. These finds prompted further field work, conducted by University of Oregon field crews, over the 2010 and 2011 field seasons, primarily in the Main and Carnivore outcrops (Fig. 2). Material collected during 2010–2011 field seasons is reposited at the John Day Fossil Beds National Monument, whereas material from 2012–2014 is reposited at the UOMNH. Outcrops at Hawk Rim are not always continuous exposure of fossiliferous rock, so each distinct area was given a locality descriptor (Fig. 2). Each locality was also correlated to the generalized stratigraphy of the Main outcrop to facilitate temporal comparisons across the site (Fig. 3). Fossil material was located by surface prospecting, with a subset of material collected by quarrying, primarily in the upper sandstone strata (Fig. 3). Sediment from several outcrops (Carnivore, Main, and Blowout) was screened for microfossils, although this collection method did not prove productive.

Outcrops were mapped onto both U.S. Geological Survey (USGS) topographic maps and Google Earth aerial imagery. Global Positioning System (GPS) locations were taken for every collected fossil using either a Garmin eTrex Legend HCx or a Trimble handheld GPS base station. Orientation and dip on bedding was measured on tuff strata when possible using a Brunton compass. Sections were measured at each locality using an Abney level and a Jacob’s staff accounting for strike and dip. The constructed composite section was based mostly on the Main outcrop (Fig. 2), with unit thickness varying between outcrops, especially in the sandstone and diatomite strata. Localities were correlated by tracing marker beds such as tuff layers, or comparing similarities in lithology.

Biostratigraphy

During field work, fossils were assigned to the stratum of origin when possible. Most specimens were found in float, so in many cases their stratigraphic assignment should be considered a lowest possible occurrence. Materials collected from dry washes and at the base of outcrops could not be assigned to an individual stratum. However, some in situ material was collected, and the topography of the site often exposed fossils in the top of saddles where they could only originate from the exposed layer. Several taxa are only represented by single identifiable specimens; therefore, a stratigraphic range at Hawk Rim cannot be generated. Known biostratigraphic ranges for each taxon present at the site were generated from the existing literature (Tedford et al., 2007). The co-occurrence of taxa was then used to generate age and NALMA estimates for Hawk Rim, as well as a better understanding of the range of time covered by deposition at the site (Fig. 4).

U/Pb and Ar/Ar Geochronology

The largest tuff in the section, which we call the Hawk Rim Tuff, was sampled for geochronology, as was another reworked tuff from lower in the section (Fig. 3). Zircon crystals were separated from the Hawk Rim Tuff by conventional density and magnetic methods. The entire zircon separate was placed in a muffle furnace at 900°C for 60 hours in quartz beakers to anneal minor radiation damage. Annealing enhances cathodoluminescence (CL) emission, promotes more reproducible interelement fractionation during laser ablation inductively coupled plasma mass spectrometry (LA-ICPMS), and prepares the crystals for subsequent chemical abrasion (Mattinson, 2005). Following annealing, individual grains were hand-picked and mounted, ground and polished to their centers, and imaged by cathodoluminescence (CL) on a scanning electron microscope. From these compiled images, the locations of spot analyses for LA-ICPMS were selected. LA-ICPMS analysis utilized an X-Series II quadrupole ICPMS and New Wave Research UP-213 Nd:YAG UV (213 nm) laser ablation system following the specific methods described in Rivera et al. (2013).

Selected crystals were plucked from grain mounts, chemically abraded using a single abrasion step in concentrated hydrofluoric acid (HFaq) at 180°C for 12 hours, and processed for isotope dilution thermal ionization mass spectrometry (ID-TIMS). Further details of ID-TIMS analysis are described by Davydov et al. (2010) and Schmitz and Davydov (2012). U-Pb dates and uncertainties for each analysis were calculated using the algorithms of Schmitz and Schoene (2007) and the U decay constants of Jaffey et al. (1971). Uncertainties are based upon non-systematic analytical errors, including counting statistics, instrumental fractionation, tracer subtraction, and blank subtraction. These error estimates should be considered when comparing our 206Pb/238U dates with those from other laboratories that used tracer solutions calibrated against EARTHTIME gravimetric standards. When comparing our dates with those derived from other decay schemes (e.g., 207Pb/206Pb, 187Re/187Os), the uncertainties in tracer calibration (0.05%; Condon et al., 2007) and U decay constants (0.108%; Jaffey et al., 1971) should be added to the external error in quadrature. Quoted errors for calculated weighted means are thus of the form ±x(Y)[Z], where X is solely analytical uncertainty, Y is the combined analytical and tracer uncertainty, and Z is the combined analytical, tracer, and 238U decay constant uncertainty.

The second dated tuff sample, the Double Tuff, did not contain zircons and thus was sent to the Oregon State Geochronology Laboratory for 40Ar/39Ar dating. 40Ar/39Ar ages were obtained by incremental heating methods using the Argus-VI mass spectrometer. Four plagioclase samples were irradiated for 6 hours in the Training, Research, Isotopes, General Atomicics: Cadmium-Lined In-Core Irradiation Tube (TRIGA CLICIT) nuclear reactor at Oregon State University, along with the Fish Canyon Tuff (FCT) sanidine (28.201 ± 0.023 Ma, 1σ) flux monitor (Kuiper et al., 2008). Individual J-values for each sample were calculated by parabolic extrapolation of the measured flux gradient against irradiation height and typically give 0.2–0.3% uncertainties (1σ). The 40Ar/39Ar incremental heat aging determinations were performed on a multi-collector Argus-VI mass spectrometer at Oregon State University that has five Faraday collectors (all fitted with 102−ohm resistors) and one ion-counting CuBe electron multiplier (located in a position next to the lowest mass Faraday collector). This allows us to measure simultaneously all argon isotopes, with mass 36 on the multiplier and masses 37 through 40 on the four adjacent Faradays. This configuration runs in a full multi-collector mode while measuring the lowest peak (on mass 36) on the highly sensitive electron multiplier (which has an extremely low dark noise and a very high peak/noise ratio). Irradiated samples were loaded into Cu-planchettes in an ultra-high vacuum sample chamber and incrementally heated by scanning a defocused 25 W CO2 laser beam in preset patterns across the sample, in order to release the argon evenly. After heating, reactive gases were cleaned up using an SAES Zr-AI ST101 getter operated at 400°C for ~10 minutes and two SAES Fe-V-Zr ST172 getters operated at 200°C and room temperature, respectively. All ages were calculated using...
the corrected Steiger and Jäger (1977) decay constant of 5.530 ± 0.097 × 10⁻¹⁰ 1/year (2σ) as reported by Min et al. (2000). For all other constants used in the age calculations, we refer to table 2 in Koppers et al. (2003). Incremental heating plateau ages and isochron ages were calculated as weighted means with 1/σ² as weighting factor (Taylor, 1997) and as YORK2 least-square fits with correlated errors (York, 1969) using the software ArArCALC version 2.6.2 (Koppers, 2002).

RESULTS

Site Geology

Strata at Hawk Rim are nearly level, with the average dip only 8°. Beds at all outcrops dip gently to the east. This dip had little effect on reconstructing the relationship of outcrops, although it was accounted for in measuring the section. The most detailed stratigraphic column, measured and described in the Main outcrop (region 4 in Fig. 2), yielded an 80-m-thick fossiliferous portion of section (Fig. 3). Although the section does continue above the Hawk Rim Tuff, the upper portion does not produce fossil material and is largely covered material between the Hawk Rim Tuff and the Rattlesnake Ashflow Tuff, some 150 m stratigraphically higher. Both tuffs sampled for geochronology are labeled, the Hawk Rim Tuff and the stratigraphically lower Double Tuff (Fig. 3). Radiometric dating indicates that this capping tuff is older than the Mascall Tuff (mapped in the type area of the Mascall Formation) by approximately 1 million years. Other previously described tuffs exist in the region, but most can be ruled out based on age and physical characteristics. Other regional tuffs include the Rattlesnake Ashflow Tuff (RAFT), Divine Canyon Tuff, Prater Creek Tuff, and several smaller ashy deposits (Jordan et al., 2004). The Hawk Rim Tuff is divided into two separate ash flow events, each massively bedded. Both upper and lower contacts are very sharp. The tuff is primarily vitric material with some lithic fragment components. The top of the lower ash flow event was sampled for radiometric dating from the Main outcrop (Fig. 2). Of note is the occasional preservation of leaves in the lower 15 cm of the tuff. Leaf-bearing localities within the tuff may represent wet depositional settings, such as ponds, over which the tuff was emplaced. This would allow for the preservation of the leaves in the base of the rapidly cooled ash, as evidenced by higher vitric content from quenching. The high degree of welding present in the tuff suggests direct air fall or pyroclastic flow emplacement without significant post-depositional reworking. No signs of bioturbation or root casts are observed in the tuff. The Hawk Rim Tuff is present only in the Main, Cone, and Carnivore outcrops (Fig. 2).

The outcrops consist of mudstones, silts, and sands, usually with some degree of paleosol development. Root traces from large woody plants are common throughout the section, and many strata also show the development of B₃ horizons. These clay-rich B₃ soil horizons indicated moderate to well-developed soils generally formed by episodic source material deposition. All clastic material is well rounded, suggesting fluvial transportation as a method of sediment emplacement. Diatomites indicate some standing water present for an extended period of time. Thin gradational layers of red-colored low-grade coal are present and contain similar plant hash and physical characteristics to those seen the lowest Mascall Formation across the John Day River from the type area (Bestland, 1998). Whereas the Mascall type area was deposited on a floodplain, the exposed palaeotopography—with higher gradient incised channels at Hawk Rim—suggests that it may have formed in narrower river valleys. The source rocks and the paleosols developed at Hawk Rim are, however, a good match with the lower Mascall Formation, indicating consistent depositional settings across the formation.

Biostratigraphy

The key defining taxon for Hawk Rim’s late Hemingfordian age is Pseudaelurus skinneri (Fig. 4). Known only from late Hemingfordian Sheep Creek localities in Nebraska (Rothwell, 2003), P. skinneri is described as an immigrant taxon confined to a narrow temporal range. All members of the unguulate fauna also make their first appearances in the Hemingfordian, with the palaeomerycids Dromomeryx and Rakomeryx both first appearing in the late Hemingfordian. Moropus is known in the Oregon Hemingfordian record, but is unconfirmed in the Barstovian (although Coombs et al., 2001, suggests that it may be present in the type Mascall). With the palaeomerycids providing an earliest age and Moropus and P. skinneri constraining a last occurrence, the fauna as a whole strongly suggests a late Hemingfordian age, in agreement with the radiometric dates. Although some taxa are more commonly known from the Barstovian, such as Dromomeryx and Merychippus, these taxa are also consistent with an earlier age assignment (Fig. 4). The age assignment from Pseudaelurus and Moropus is corroborated by the radiometric dates, with nearly all of the fossils constrained between dates of 16.4 and 16.2 Ma. Compared with the Barstovian NALMA or even the early Hemingfordian, the latter half of the Hemingfordian is one of the least sampled NALMAs in the Pacific Northwest (Tedford et al., 2004).

Canids are reputed to be particularly good biostratigraphic indicators in the region (Wang et al., 1999) and have already been used for regional biostratigraphy (Orcutt et al., 2011). Both Paratomarctus and Tephrocyon are known from the earliest Barstovian (Wang et al., 1999; Tedford et al., 2004), and thus represent a new first appearance datum (FAD) at Hawk Rim, and underscore how regional endemicity in areas of ecological heterogeneity can result in range expansions. Furthermore, the beaver Monosaulax has only been found from the beginning of the

FIGURE 2.  Map of Hawk Rim localities. Topographic map courtesy of the USGS, quadrangles Oregon Arrowood Point and Liggett Table. Shaded sections denote the localities of fossil-bearing areas at Hawk Rim. Areas are numbered as follows: 1, Blownout locality (JDNM 271); 2, Brit locality (JDNM 272); 3, Carnivore locality (JDNM 269 and UO 4360); 4, Main locality (JDNM 267); 5, Cone locality (JDNM 268); 6, Front Hills locality (JDNM 270).
FIGURE 3. Simplified stratigraphic column as seen in the Main outcrop locality of Hawk Rim. All other localities are correlated to this stratigraphy, as shown on the right. Stratigraphic ranges of taxa taken for all localities.
FIGURE 4. Plot of temporal ranges of Hawk Rim taxa. Species or genera ranges denoted with black bars, taxa extending into earlier NALMAs shown with a downward arrowhead. Gray bar represents the authors’ preferred age interpretation for the Hawk Rim deposits based on geochronology.
Barstovian through the end of the Barstovian (Korth, 2001), with two poorly dated sites possibly representing Hemingfordian occurrences (Bailey, 2004). *Monosaulax* at the late Hemingfordian Hawk Rim possibly corroborates the two other reputed Hemingfordian occurrences. The early Barstovian marks the last occurrence of canids such as *Cynarctoides* (Wang et al., 1999) as well as the equid *Desmatippus* and paleomerycid *Rakomeryx* (Tedford et al., 2004), with all of these taxa more commonly known from the late Hemingfordian, and therefore strengthening the biostratigraphic assignment to the Hemingfordian.

**U/Pb and Ar/Ar Geochronology**

Hawk Rim possesses several tuff beds containing minimally reworked volcaniclastic sediments. Flow deposits greater than 1 m in thickness potentially indicate a nearby volcanic source; however, further work matching tuffs based on physical and geochemical analyses are necessary to understand volcanic sources and relationships in the region. The Hawk Rim Tuff is crystal rich, yielding an abundant, homogeneous zircon crystal population of elongate prismatic grains. Cathodoluminescence images were similarly homogeneous (Fig. S1). The LA-ICPMS spot ages (Table S1) included a minor group (11) of Cretaceous to Paleogene crystals and a major population of Miocene grains, the latter of which were targeted for CA-TIMS analysis as the potentially primary pyroclastic population. All analyses yielded concordant and equivalent U-Pb dates (Table S2), with a weighted mean $^{206}$Pb/$^{238}$U age of 16.260 ± 0.009 (0.012) [0.021] Ma (n = 8; Mean Squared Weighted Deviation (MSWD) = 2.13) (Fig. 5), which is interpreted to estimate the eruption and depositional age of the volcanic deposit. Because this date is from the tuff capping the fossiliferous portion of the section, all fossils reported are no younger than this age. This places the Hawk Rim locality solidly in the late Hemingfordian or earlier.

Incremental step-heating of the plagioclase from the Double Tuff yielded reproducible $^{40}$Ar/$^{39}$Ar ratios over the last 15 of the 23 heating steps, representing >95.5% of $^{39}$Ar released from the sample (Fig. 6; Table S3). The corresponding plateau age is calculated as 16.436 ± 0.031 [0.053] Ma (MSWD = 1.16), which is interpreted as the best estimate of the eruption and depositional age of the tuff. This interpretation is supported by the inverse isochron age of 16.43 ± 0.04 [0.06] Ma, with a calculated initial $^{40}$Ar/$^{39}$Ar of 296.35 ± 5.4, in agreement with atmospheric composition. Given the accuracy of the intercalibration of U-Pb and $^{40}$Ar/$^{39}$Ar chronometers using the FCT sanidine monitor age of Kuiper et al. (2008), these two bracketing ages constrain the intervening 70 m of rock accumulation to within 176 ± 57 ka. This implies a rock accumulation rate averaging 0.4 mm per year at Hawk Rim and neatly constrains nearly all fossil material to within the late Hemingfordian NALMA.

**SYSTEMATIC PALEONTOLOGY**

*Family CAMELIDAE* Gray, 1821

**Occurrence**—JDNM locality 267.

**Referred Material**—JODA 15018, right astragalus; UOMNH F-60143, left astragalus.

**Description**—Specimen JODA 15018 was collected from fluvial sandstone and shows some evidence of minimal transport, resulting in somewhat worn edges, whereas UOMNH F-60143 is complete. Standard measurements were taken for identification (DeGusta and Vrba, 2003). Although size is not generally a defining feature, the overall small dimensions precluded many of the possibilities, such as the uniformly larger paleomerycids. The trochlear keels are oriented parallel to the length of the bone, indicating that the astragali belonged to a small artiodactyl. Both trochlear keels are of nearly the same length, ruling out artiodactyl families such as Camelidae. Overall, the shape is roughly rectangular, unlike the ventral flexed shapes of the Tayassuidae. Antilocaprid astragali from Red Basin (UOMNH F-4950, UOMNH F-30987, UOMNH F-7459) and the type area of the Mascall Formation (UCMP 1726) were used as comparison to verify the identification. The comparative material is only identified as ‘antilocaprid,’ but both formations have previously only had *Merycodus* described.

**Discussion**—Although astragali can be highly diagnostic in artiodactyls, they must be associated with skull or dental material for initial identification. Unfortunately, antilocaprids are often an uncommon member of faunas; thus, identified material for comparison is limited. The astragus appears not only smaller, but has some differences in the morphology of the lateral side as compared with *Merycodus*. Although *Merycodus* is the only previously described antilocaprid from the Mascall Formation and Red Basin (Downs, 1956; Shotwell, 1968), these smaller specimens may represent a new occurrence of *Submeryceros* or *Merriamoceros*.

**Family ANTilocapridae** Gray, 1866

**Occurrence**—JDNM locality 267, JDNM 271, and JDNM 272.

**Referred Material**—JODA 14975, canine; JODA 14988, tooth fragments; JODA 15066, tooth fragment; JODA 15075, tooth fragment; JODA 15118, tooth fragments; JODA 15127, tooth fragments.

**Description**—Although numerous specimens diagnostic as camelid have been discovered at Hawk Rim, none of the material can be assigned to a genus. All material is from a relatively small camelid, and size is consistent through all samples. Dental
material was assigned to the Camelidae on the basis of labial ribs in the middle of the labial portion of each tooth, high crowns, and lack of cementum (Honey et al., 1998). The teeth are also higher-crowned and larger than many of the other artiodactyls and perissodactyls of the time. The only complete tooth, a canine, is small in size (length = 12.15 mm, width = 9.10 mm, crown height = 16.08 mm), indicating that the camelid at the site was small in overall stature.

**Discussion**—The consistency in size indicates that all material likely came from the same species, which appears to be the only camelid present at the locality. The lack of llama buttresses on the tooth fragments indicates that the species was a camelin camelid (Webb, 1965). A small camelid is also present in Red Basin, but is a sparsely represented component of the fauna and thus is also unidentified beyond Camelidae (Shotwell, 1968). Miolabine camels are found in the Mascall Formation (Downs, 1956) and represent the most likely candidate, despite the younger age of the Mascall type fauna. Camels of this age are difficult to identify, in part because the family is overdue for revision (Honey et al., 1998).

**Family MERYCOIDODONTIDAE** Thorpe, 1923

**Occurrence**—JDNM 272.

**Referred Material**—JODA 15065, left M1.

**Description**—Although a complete tooth is preserved, the fact that oreodont taxonomy is poorly resolved and largely based on complete skulls prevents generic-level identification. The upper molar is selenodont and low-crowned. Macrowear is angular, consistent with a browsing herbivore. The tooth is 13.3 mm long and 13 mm wide. Crown height, measured from the base of the enamel to the juncture between lophs, is 5.8 mm. The tooth has a cingulum on the lingual side, which is weakly continuous onto the anterior and posterior sides of the tooth. The protocone is rounded and extends farther lingually than other cusps.

**Discussion**—Although morphologically consistent with *Ticholeptus* (Bryant, 1991), JODA 15065 is considerably smaller than comparable specimens from Red Basin (UOMNH F-22192; length = 15.09 mm, width = 16.23 mm, crown height = 4.13 mm). Similarities to both Red Basin and Mascall specimens support the probable diagnosis as *Ticholeptus*. However, the specimen’s small size and the limited material preclude a positive diagnosis. More material would be needed to facilitate identification past family level.

**Family PALAEOMERYCIDAE** Lydekker, 1883

**Genus DROMOMERYX** Douglass, 1909

**Occurrence**—JDNM 267, JDNM 268, and JDNM 270.

**Referred Material**—JODA 14968, distal humerus, distal metapodial; JODA 15090, tooth fragments; JODA 15145, p2.

**Description**—Most preserved material is fragmentary and is less common than the other palaeomerycid *Rakomeryx* or the equid genera. The distal humerus and metapodial were identified by comparisons with *Dromomeryx borealis* specimen UCMP 1486 from the Mascall Formation UCMP locality 3059. The orientation of the troclear keels on the humerus and the size are consistent between the specimens, supporting the diagnosis as belonging to *Dromomeryx*. On the metapodial, the metatarsal gully is fully closed and the distal articular surfaces have complete phalangeal keels (Prothero and Liter, 2007). Red Basin *Dromomeryx* specimens (UOMNH F-20695, UOMNH F-20512, UOMNH F-20673) were used as comparisons to facilitate the identification of the Hawk Rim astragalus. Standard measurements (DeGusta and Vrba, 2003) were taken on both the Red
Basin and Hawk Rim astragali. The Hawk Rim specimen of *Dromomeryx* is the same size as one Red Basin specimen (UOMNH F-23363) but smaller than all other measured samples (Table 1). Dental material was compared with specimens from both the Mescal Formation and Red Basin. The posterior portion of the premolar is preserved and has the same crescent-shaped facet opening lingually, with the most posterior enamel juncture opening posteriorly and then turning 100° to open lingually. The ‘E’ shape in the protoloph, protocone, and hypocone of the posterior premolar is indicative of an artiodactyl, and morphological dimensions, as well as the articular surface, were identified as consistent with *Dromomeryx*. Although not complete, the width measurement for the second premolar was 7.5 mm and the projected total length was 15 mm.

**Discussion**—*Dromomeryx* represents a common member of both the Mescal type area (Downs, 1956) and Red Basin (Shotwell, 1968). Although overall the collected material from Hawk Rim is too limited to generate robust abundance data, the percentage of ungulate material assigned to *Dromomeryx* indicates that it was not a common member of the herbivore community as preserved up to this point. Furthermore, material from Hawk Rim suggests that the species present was, on average, of much smaller stature than is present in the Mescal type area or in Red Basin (Table 1). The observed degree of potential size evolution could have occurred over the time differential between localities. Lastly, Hawk Rim is also significantly west of Red Basin and the Mescal type area and the difference could reflect size variation over geographic gradients. *Dromomeryx* is currently monotypic, with only one recognized species, *D. borealis* (Prothero and Liter, 2007). Considerable size variation exists among specimens assigned to this species. The Hawk Rim specimens fall within the range of variation seen at other sites, but are consistently in the smallest range of observed measurements. More material is needed from Hawk Rim, as well as a reevaluation of variation within *Dromomeryx* as a whole, to consider its species-level taxonomy.

**Genus RAKOMERYX Frick, 1937**

**RAKOMERYX SINCLAIRI** (Matthew, 1918)

**Occurrence**—JDNM 267, JDNM 268, JDNM 269, and JDNM 270.

**Referred Material**—JODA 15034, cannon bone; JODA 15043, lower premolar; JODA 15073, lower molar; JODA 15086, astragalus; JODA 15143, cubonavicular; JODA 15152, m1 and tooth fragments.

**Description**—Material from *Rakomeryx* is slightly more common than the larger *Dromomeryx* at Hawk Rim. Even given the limited total collection, this differs from Red Basin localities where *Dromomeryx* specimens outnumber *Rakomeryx* by an order of magnitude (Shotwell, 1968). Although *Rakomeryx* material for comparison is limited, some dental material from Red Basin was used to facilitate comparisons. The cannon bone, or fused metacarpal, was identified by comparison with AMNH 53995, AMNH 53995A, AMNH 53992A–D, and AMNH 53994A–E, all material from the Sinclair Quarry (also known as Princeton locality 1000C) from the Hemingfordian. All relationships between morphological dimensions, as well as the articular surface, were identified as consistent with *Rakomeryx*, but more robust than *Subdromomeryx* and smaller than *Dromomeryx*. This comparison also held true for the cubonavicular. The fusion of metapodials III and IV was indicative of an artiodactyl, and the size precluded several other animals. It was morphologically distinct, with a different shape of the articular surface than camels, as shown by comparison with UOMNH F-8702. Dental elements were identified by comparison with material from Red Basin (UOMNH F-22147 and UOMNH F-22146). The proportions of the astragalus are similar to those seen in the larger *Dromomeryx*, but all measured dimensions (DeGusta and Vrba, 2003) were smaller than those observed in either Hawk Rim or Red Basin *Dromomeryx* (Table 2).

**Discussion**—Dental material from Hawk Rim, although limited, seems to be of a similar size to that from Red Basin. Unlike Red Basin, or the Mescal Formation type area, *Rakomeryx* represents a common member of the ungulate fauna. The genus is

| Specimen number | LM (mm) | TD | TI | TP | LL | WD | WI | LI |
|-----------------|--------|----|----|----|----|----|----|----|
| JODA 15086      | NA     | 15.56 | 15.64 | 12.14 | 32.92 | 18.44 | 19.03 | 26.88 |
| JODA 15006      | 34.82  | 15.96 | 18.01 | 13.85 | 37.36 | 23.68 | 22.6 | 29.79 |
| UOMNH F-23363   | 36.46  | 18.46 | 18.1 | 13.75 | 39.55 | 24.28 | 24.09 | 32.47 |
| UOMNH F-20596   | 43.62  | 22.75 | 23.21 | 16.81 | 47.69 | 27.06 | 26.89 | 36.73 |
| UOMNH F-20570   | 41.79  | 20.44 | 22.14 | 14.36 | 47.25 | 27.36 | 26.52 | 36.02 |
| UOMNH F-22103   | 41.87  | 20.33 | 23.26 | 17.19 | 46.33 | 27.18 | 26.06 | 36.2 |
| UOMNH F-22107   | 46.46  | 23.63 | 25.44 | 18.53 | 50.48 | 31.97 | 30.85 | 40.51 |
| UOMNH F-22102   | 43.63  | 21.93 | 22.61 | 17.85 | NA    | 38.05 | 28.54 | 37.03 |
| UOMNH F-22101   | 43.52  | 23.08 | 23.9 | 17.97 | 48.56 | 31.92 | 29.58 | 37.88 |

**Table 1.** Complete faunal list for Hawk Rim.

| Class          | Order         | Family          | Genus     | Species |
|----------------|---------------|-----------------|-----------|---------|
| Mammalia       | Artiodactyla  | Antilocapridae  | Dromomeryx|         |
|                |               | Camelidae       | Rakomeryx | sinclairi |
|                |               | Merycoodontidae |          |         |
|                |               | Palaeomerycidae |          |         |
|                | Carnivora     | Amphicoenidae   |          |         |
|                |               | Canidae         |          |         |
|                |               | Felidae         |          |         |
|                |               | Mustelidae      |          |         |
| Lagomorpha     | Perissodactyla | Chalicotheriidae|          |         |
|                |               | Equidae         |          |         |
|                | Rodentia      | Castoridae      |          |         |
|                |               | Monosaulax      |          |         |
|                |               | Merychippus     |          |         |
|                |               | Deinotocyon     |          |         |
|                |               | Sciuridae       |          |         |

**Table 2.** Standard measurements of artiodactyl astragali from DeGusta and Vrba (2003) for comparing the size and morphology of Hawk Rim palaeomerycid astragali.
monotypic and can be diagnosed based on the complete (although very worn) teeth discovered at Hawk Rim.

**PALAEOMERYCIDAE, indet.**

**Occurrence**—JDNM 267.

**Referred Material**—JODA 15042, molar, incisors, canine, jaw fragment.

**Description**—Collected material was all from the same individual and represents the anterior portion of a mandible. One incisor was found still in place in an alveolus in the small jaw fragment. Other incisors were found in association, as well as the canine and molar. The molar is extremely worn, suggesting that the individual may have been old at the time of death. The canine was diagnostic as belonging to the Tayassuidae because of the occlusal wear pattern, with distinct ‘self-sharpened’ edges (Harris and Liu, 2007). Although heavily worn, the bunodont cusp morphology and two distinct lophs of the molar were also characteristic of a tayassuid. The incisors are peg-shaped and very worn.

**Discussion**—The level of wear on this specimen precluded identification. Furthermore, although the canine and incisors are indicative of a tayassuid, little morphological variation exists between genera. The Barstovian Mascall type area, the Railroad Canyon Sequence (late Hemingfordian to Barstovian in Idaho), and Red Basin all contain tayassuids (Shotwell, 1968; Barnosky et al., 2007; Fremd, 2010). However, Railroad Canyon and the type Mascall area contain material identified as Cynorca, whereas Red Basin contains Prosthennops. Although Railroad Canyon is an early Barstovian fauna located in eastern Idaho, and thus farther away than other faunas used for comparison, it shares faunal similarities with Hawk Rim. With limited morphological differentiation between these genera, it is difficult to discriminate them without more extensive material. Furthermore, recent reevaluation of Mascall material has indicated the presence of Prosthennops in addition to the previously identified Cynorca (Maguire, 2014). With only one worn molar, it is also difficult to tell its position in the jaw. The molar appears to be closer to the smaller size range observed in Cynorca than the larger genera such as Prosthennops and Dysochlys (Barnosky et al., 2007). More precise assignment is further confounded by the suggestion that Cynorca is highly paraphyletic and in need of extensive phylogenetic reevaluation (Wright, 1998).

Order CARNIVORA Bowdich, 1821

Family AMPHICYONIDAE Haeckel, 1866

Genus **AMPHICYON** (Lartet, 1836)

**AMPHICYON** cf. **A. FRENDENS** Matthew, 1929

**Occurrence**—JDNM 267.

**Referred Material**—JODA 15058, left first metacarpal.

**Description**—Recovered material is limited to a left first metacarpal. The complete bone is extremely robust, representing a large, muscular animal. The bone is relatively short compared with its width and does not taper. The bone likely came from an older individual because the plantar surface shows evidence of low-grade arthritis, with the development of small subchondral cysts.

**Discussion**—Amphicyonids have characteristically short robust manus bones not exhibiting any lateral compression such as in canids (Hunt, 2003). Amphicyon is characterized by very robust metapodials and is well known in the Middle Miocene (Hunt, 1998). *Pliocyon* and *Ischyrocyon*, two other Miocene amphicyonids, were ruled out because they are both too gracile for the Hawk Rim specimen. *Amphicyon* also shows a range of overlapping sizes and is found in the Mascall type area (Downs, 1956) and Red Basin (Shotwell, 1968). The Hawk Rim specimen is morphologically and morphometrically very consistent with an unpublished partial skeleton from Virgin Valley; however, that material has not yet been identified at the generic level. Species-level assignments were made largely on size. *Amphicyon ingens* has the largest limb proportions (Janis and Wilhelm, 1993), and although manus bones were not available for comparison, the relative difference in limb length between *A. ingens* and *A. frendens* (Janis and Wilhelm, 1993) suggests that *A. ingens* is too large to match the Hawk Rim specimen. Not only are other species of *Amphicyon* (such as *Amphicyon galushai*) generally not found during the late Hemingfordian, but *A. galushai* is also substantially smaller than *A. frendens* (Hunt, 2003).

Family CANIDAE Fischer von Waldheim, 1817

Genus **CYNARCTOIDES** McGrew, 1938

**CYNARCTOIDES ACRIDENS** (Barbour and Cook, 1914) (Fig. 7A)

**Occurrence**—JDNM 272.

**Referred Material**—JODA 14964, right m1.

**Description**—This molar belonged to a very small canid. The paraconid is broken off, trigonid width 4.1 mm and talonid width 4.5 mm, within the reported range 2.5–4.0 mm (trigonid width), and 3.1–4.8 mm (talonid width), respectively, for *C. acridens* (Wang et al., 1999). Diagnostic of the species, the molar is relatively high-crowned, with conical cusps on the lower molars, compared with other species of *Cynarctoides*. The metaconid is high in relationship to other cusps, with an enlarged protostylid. Overall, the tooth is consistent with the elongate, narrow teeth found in *Cynarctoides*. Furthermore, the tooth is indicative of an animal that was quite hypocarnivorous, as evidenced by the relative enlargement of the talonid basin and reduction of the shearing facets. *Cynarctoides* was more hypocarnivorous than other related genera such as *Pliocyon* and *Cynarctus*. Although still a small canid, *C. acridens* is the largest species and type species of the genus (Wang et al., 1999). Unlike other species in the genus, *C. acridens* has a metastylid on the m1 and a more pronounced protostylid than species such as *C. gawnae*. Furthermore, the characteristic enlarged protostylid of the genus is hypertrophied, resulting in the reduction of the protoconid. The Hawk Rim specimen exhibits the highly derived dental morphology of the last species of this genus.

**Discussion**—The genus is known from the Whitneyan to the early Barstovian in both the Great Plains and the west. Hawk Rim represents the first occurrence of this species in Oregon, with a previous distribution limited to Nebraska, Wyoming, and New Mexico (Wang et al., 1999). This species was the
longest-lived as well as one of the most geographically widespread of all species of Cynarctoides. Therefore, it is unsurprising to discover this small borophagine canid in Oregon.

Genus **Paratomarctus** Wang et al., 1999

**Paratomarctus temerarius** (Leidy, 1858) (Fig. 7B)

**Occurrence**—JDNM 271.

**Referred Material**—JODA 14998, left M1.

**Description**—Only a single tooth has been recovered from this species; however, it is a highly diagnostic element in canids. The most important feature indicating assignment to this genus is the strongly pronounced lingual cingulum, which extends much further anteriorly than in other genera. *Paratomarctus temerarius* is the smaller of the two species of Paratomarctus. The Hawk Rim specimen has a length of 9.0 mm and a width of 13.3 mm, measurements consistent and within the known range of *P. temerarius* (average M1 length 11.7 mm, average M1 width 13.8 mm) but not *Paratomarctus euthos* (Wang et al., 1999).

**Discussion**—*Paratomarctus* is known from the late Hemingfordian to the late Clarendonian (Wang et al., 1999). Although *P. temerarius* is known from the early Barstovian of Oregon (Gazin, 1932), Hawk Rim represents the first occurrence in the Mescal Formation (the only canids previously recorded were *Tomarctus* and *Tephrocyon*; Fremd, 2010) and the first occurrence in the late Hemingfordian outside of Nebraska (Wang et al., 1999). Although both the length and width measurements are within the known range for the species, the length was at the known minimum whereas the width was at the known maximum.

Genus **Tephrocyon** Merriam, 1906

**Tephrocyon rurestris** (Condon, 1896) (Fig. 7C)

**Occurrence**—JDNM 269 and JDNM 271.

**Referred Material**—JODA 15142, maxilla fragment with fourth premolar and first molar; JODA 14135, upper fourth premolar.
Description—The maxillary fragment with two perfectly preserved teeth facilitated a definitive identification of *T. rurestris*. As a monotypic genus, *Tephrocyon* is quite distinct from all other contemporary canids. Much larger than its evolutionary predecessors and contemporaries (Wang et al., 1999), *Tephrocyon* immediately stands out. The M1 possesses a distinct metaconule and is less high-crowned than other genera. The holotype specimen (UOMNH F-23077), a complete skull from the Mascall Formation type area, offers a basis for morphological comparisons. The morphology of Hawk Rim specimens was consistent not only in size, but in all observed morphological details. This comparison also holds true with Red Basin specimens published by Shotwell (1968). The teeth are robust in comparison with other genera and Hawk Rim canids as well. The length of the M1 is 12.2 mm, whereas the width is 14.4 mm. This is very close to the average values reported by Wang et al. (1999) of 12.1 mm and 15.0 mm for length and width.

Discussion—*Tephrocyon rurestris* is the only canid previously known from the Mascall Formation (Downs, 1956; Fremd, 2010). It is also well known from Red Basin (Shotwell, 1968). Although *T. rurestris* is known from the early Barstovian of Oregon, the Hawk Rim specimen represents the first occurrence of the genus in the late Hesperian. As the only canid in the region during the early Barstovian, it may have been a more common member of local faunas than the smaller canines and may have played a role as one of the top predators. With its adaptations for increased bone crushing (Wang et al., 1999), scavenging may have constituted an important portion of its diet.

Family FELIDAE Fischer von Waldeheim, 1817
Genus PSEUDAELURUS Leidy, 1858
PSEUDAELURUS SKINNERI Rothwell, 2003
(Fig. 7D)

Occurrence—JDNM 269.
Referred Material—JODA 14977, right mandibular ramus with broken c, p3, p4, and m1.
Description—A nearly complete right mandibular ramus of a felid was recovered from Hawk Rim. The canine is broken, leaving only the root and very base of the tooth. The single-rooted second premolar is missing. However, the third and fourth premolars, as well as the first molar, are present and well preserved. The p3 and p4 are situated in line with the tooth row, slightly labial to the inset alveolus of the missing p2. The m1 has the characteristic bow-tie shape of the paraconid and protoconid seen in true felids, but also retains small metaconid and talonid cusps. The ascending posterior ramus of the jaw is broken and missing. The dentary is overall slender and gracile. There is a large mandibular foramen, positioned ventral to the coronoid process. Although the ramus is broken off, the remaining bone hints at a highly upright position of the ascending ramus. The canine is missing the tip, but the remaining part of the tooth clearly shows an ovate cross-section, which is characteristic of *P. skinneri* compared with the rounded cross-section seen in other species of *Pseudaelurus*. The second premolar is single-rooted, a characteristic also found only in this species.

Discussion—Although not the earliest true felid, *Pseudaelurus* is the first felid to reach North America and as such, still possesses several basal felid characteristics. Characteristics diagnostic of the genus are the absence of the first premolar and the second molar. The first molar still retains a highly reduced metaconid and talonid, features lost in later genera. Unlike later felids, the second premolar is still retained, but has undergone severe reduction, as can be seen in the single-rooted alveolus on the Hawk Rim specimen. North American *Pseudaelurus* differ from European and Asian species in that they have a shorter total tooth-row length, the first molar possesses a taller protoconid and a more reduced metaconid and talonid, and the tall protoconid is consistently taller than the paraconid, as opposed to what is seen in *Pseudaelurus lorteti* (Rothwell, 2003). North American species also possess a fourth premolar with a protocone that projects at an obtuse angle anterolingually (Rothwell, 2003). The upright orientation of the ascending ramus is similar to *Pseudaelurus validus* (late Hesperian, early Barstovian) as well as *P. skinneri*, but *P. validus* is a much larger species. North American species can be most readily distinguished by size. The length of the first molar in the Hawk Rim jaw is 12.9 mm, with the observed range for the species being 11.5–13.8 mm (Rothwell, 2003).

*Pseudaelurus* is only known from generic-level records in Oregon. *Pseudaelurus lorteti* and *P. skinneri* are considered the oldest true felids in North America, but their closest relatives are confined to Europe, with currently no Asian distribution. Most Oregon material is predominately from the Hemphillian Black Butte localities. Although the Mascall Formation has supposedly yielded the taxon (Fremd, 2010), no curated material was located, nor is any published. Material from Red Basin is fragmentary and limited to two individual teeth and some postcranial material (Shotwell, 1968). Because dental material from Red Basin UO 2945 was limited to upper teeth, a direct comparison with the Hawk Rim specimen is impossible. However, material from Red Basin seems to be from a larger individual than the specimen from Hawk Rim. The Hawk Rim jaw represents not only the first *Pseudaelurus* specimen from Oregon assignable to the species level, but also a geographic range extension for the species.
The alveoli of the p3 are aligned parallel to the tooth row and show no rotation of the premolars associated with crowding of the teeth (Smith et al., 2015). The alveoli of p2 are not preserved, so the degree of rotation cannot be estimated. The canine seems to fit against the anterior portion of the anterior mandible section, suggesting little space for a p1 to be present, but this assertion would require more complete material.

Dental morphology is consistent with a hypercarnivorous animal. The dentition is robust, with reduction of the crushing portions of preserved teeth as well as accessory cusplets associated with shearing on the premolars. All preserved premolars and alveoli are double-rooted. The canine tooth is 9.8 mm long and 6.8 mm wide, with a crown height of 12.9 mm measured from the enamel-dentine junction to the slightly worn tip of the cusp.

FIGURE 8. *Watay tabutsigwii*, JODA 15060, partial left mandible. A, labial view; B, occlusal view of mandible with teeth in place, with occlusal view of premolar and partial first molar; C, lingual view of mandible and teeth. Note the ‘blood channel’ visible on the posterior side of the labial view of the canine diagnostic of hypercarnivorous mustelids. The highly robust nature of the mandible is displayed in the mandibular bone. Scale bar equals 1 cm.
There is wear along the lingual channel, as well as the point of the tooth. Although robust, the canine does not broaden significantly towards the base as in Brachyopsalis (Galbreath, 1955). The premolars possess both a cingulum and two accessory cusplets. The length, width, crown height to the highest cusp, and crown height to the second accessory cusplet were measured for the premolars and are as follows: p3 anteroposterior length = 7.0 mm, width = 4.2 mm, crown height to highest cusp = 3.9 mm, and crown height to middle cusplet = 3.7 mm. The preserved portion of the first molar reveals a very short, highly trenchant talonid with the basin opening lingually, and is 5.9 mm high from the enamel-dentine junction to the highest preserved portion of the crown height. The hypoconid is reduced to the point of being virtually absent. Wrapping around the tooth is a pronounced cingulum, visible on labial, lingual, and posterior portions of the m1. The alveolus for the single-rooted m2 is angled forward and relatively small, implying a small m2 in the specimen, typical for a mustelid (Baskin, 1998).

**Diagnosis**—Watay is characterized by a shortened robust mandible that is deepest posterior to the p3. The genus possesses premolars with two accessory cusplets decreasing in size posteriorly. In the m1, the talonid basin is highly trenchant and roughly ovate in shape. The alveolus of the m2 is reduced and angled toward the anterior portion of the mandible. The canine is curved somewhat posteriorly, ovate in cross-section, and broadens slightly posteriorly at the base. Watay tabutsigwii is large in size for a mustelid, comparable to that of modern Galictis vittata. The p2–p4 are double-rooted, and the p4 lacks any additional rootlets. Both the p2 and p3 possess a strong cingulum, most notable on the labial and lingual sides of the tooth. The m1 talonid also contains a pronounced cingulum visible on both the labial and lingual portions of the tooth. The mandible is shortened, but tooth crowding does not occur to the degree that the posterior teeth are rotated.

**Discussion**—Although other mustelids exhibit some features shared with Watay, such as the trenchant talonid seen in Sthenictis, no described mustelid matches all characters observed in the Hawk Rim specimen. Watay differs most obviously from many Miocene mustelids in size, with taxa such as the Oligobuninae not reaching the large size seen in the Hawk Rim specimen (Baskin, 1998). The assignment to the Ischyricthinae derives from the highly trenchant talonid on the m1, with all members of that group displaying a semitrenchant to trenchant talonid of the m1 (Smith et al., 2015). The trenchant talonid is seen in hypercarnivorous mustelids such as Sthenictis, but assignment to this genus is precluded by the very short anteroposterior length of the talonid in the first molar in the Hawk Rim specimen; Sthenictis is characterized by an elongate, narrow m1 talonid. Mionictis is equally untenable, because that genus possesses a much less pronounced cingulum and a more dominant hypoconid invading the talonid basin. Hoplicictis, and many other mustelids, lacks accessory cusps on the premolars. Oligobunis is one of the few large Hemingfordian mustelids, but is characterized by posteriorly broadening premolars and the presence of a notable hypoconid on the m1, both of which are characters not observed in the Hawk Rim specimen. Neoduaetelis is another large mustelid known from the Barstovian of Nevada, but this genus is equally untenable because of its characteristic rugose enamel especially apparent on the m1 talonid (Smith et al., 2015). The European Ischyricthys shares the greatest number of similarities with Watay and may represent the parent taxon. Although never actually recorded in North America, it is considered an immigrant taxon from Europe (Oiu, 2003). The most similar North American mustelids are all grouped into the Ischyricthinae, reflecting this relationship. Ischyricthys, however, never achieved reduction of the talonid to the extent seen in Watay. Most species also have less prominent accessory cusps on the premolar (Ginsburg, 1961; Petter, 1963), with overall more robust premolars that are also more pyramidal in shape (Ginsburg and Morales, 1992). The specimen shares strong similarities with the modern Galictis, such as a trenchant ovate talonid and a cingulum on both the posterior m1 and premolars and may represent an evolutionary stepping stone along the route from their European ancestry to South America, where they are found today. Derived Galictini are represented in the North American fossil record from the Blanca Hagerman Fossil Beds exclusively (Bjork, 1970), but the Galictini are known from the Hemphillian in the Blanca in the intermontane west, including the Oregon occurrences of Mionictis.

Order LAGOMORPHA Brandt, 1855
Family LEPORIDAE Fischer von Waldheim, 1817

**Occurrence**—JDNM 269 and JDNM 271.
**Referred Material**—JODA 15044, proximal tibia; JODA 15078, calcaneum.
**Description**—With only a water-worn calcaneum and a broken proximal end of a tibia to refer to this family, generic-level identification was not possible. Material was identified as belonging to a leporid through morphological comparisons with modern leporid skeletal material (UMONH R-8456 and UOMNH R-8271). Both the elongation of the tibial shaft and posterior portion of the calcaneum were consistent with the assignment as a leporid, but would have been inconsistent with ochotonids.

**Discussion**—More material is needed. Both the type area of the Mascaill Formation and Red Basin contain Hypolagus as the only identified leporid present (Downs, 1956; Shotwell, 1968). The Hawk Rim material may also belong to this genus and would be consistent with the observed size range for the genus.

Order PERISSODACTYLA Owen, 1848
Family CHALICOTHERIIDAE Gill, 1872
Genus cf. MOROPUS Marsh, 1877

**Occurrence**—JDNM 267.
**Referred Material**—JODA 15059, partial first upper molar.
**Description**—Very large size of the specimen precludes most mammals. Only the labial portion of the tooth is preserved, with a small portion of the infolded central enamel area from the anterior portion of the tooth also attached. The length of the tooth is 61 mm. Although the lingual three-quarters of the tooth is missing, it is possible to estimate the anteroposterior width of the tooth at 37 mm. The ‘W’-shaped ectoloph of the tooth clearly indicates a perissodactyl; however, the dimensions of the tooth make it far larger than even rhinocerotids of the time period. Furthermore, the enamel edge is also lacking the prominent perykymata seen in the enamel of rhinocerotids. Tooth morphology and the presence of the infolded enamel portion, or post fossette (Coombs, 1978), of the tooth identify it as a chalicother and specifically Moropus (Coombs, 2004).

**Discussion**—Although Moropus was noted from the Mascall Formation by Marsh, the specimen he described was subsequently lost (Coombs et al., 2001). All other John Day Basin material belonging to Moropus has been collected from the Haystack and Kimberly members of the John Day Formation (Fremd, 2010). The Hawk Rim specimen therefore represents the youngest known specimen of the genus in the area (Coombs et al., 2001). The Hawk Rim specimen is also larger than any described specimen of Moropus. It may either represent a new species or indicate greater morphological variation than previously recorded. More material would be needed to draw conclusions regarding the phylogenetic affinities of the Hawk Rim specimen.
Family EQUIDAE Gray, 1821
Genus ARCHAEOHIPPUS Gidley, 1906

**Occurrence**—JDNM 267, JDNM 268, JDNM 269, and JDNM 271.

**Referred Material**—JODA 14991, metapodial; JODA 15004, cubonavicular, phalanx, upper molar; JODA 15040, first premolar; JODA 15053, phalanx; JODA 15061, upper cheek tooth; JODA 15071, phalanx and lower cheek tooth; JODA 15081, astragalus; JODA 15082, astragalus; JODA 15104, phalanx.

**Description**—All listed material was easily assignable to Archaeohippus on the basis of its extremely small size and morphology differing from contemporary equids. Size, in addition to morphological modifications to the limb dimensions, is generally recognized as valid grounds for assigning equid material to this genus (Janis et al., 1998; MacFadden, 1999; O’Sullivan, 2003; Barnosky et al., 2007). In addition to small size, the genus possesses low-crowned teeth. The limb bones are not only small, but highly gracile (O’Sullivan, 2003), as can be seen in the delicate second and fourth phalanges of this genus found at Hawk Rim. The phalanges also display the reduced tridactyly linking this primitive-looking horse to merychippine-grade horses (O’Sullivan, 2008), with the stature secondarily reduced through phyletic dwarfing (MacFadden, 1999). The teeth of this genus are not only small and low-crowned, but also have cementum and crochets in the upper teeth.

**Discussion**—Archaeohippus is known both from the Mescal Formation (Downs, 1956) and from Montana’s Barstovian Railroad Canyon fauna (Barnosky et al., 2007), but is unrecognized in the geographically intermediate Red Basin fauna. At both other regional sites, Railroad Canyon and the Mascall Proper, this small equid is an uncommon member of the fauna. At Hawk Rim, Archaeohippus (although still limited) is no less common than other equids or artiodactyls. Although some of this frequency may reflect the ease in identifying its remains from more fragmentary pieces than is possible for other genera, the taxon still represents a more substantial portion of the fauna than at other sites. Because Archaeohippus is thought to be a browsing taxon (MacFadden, 1999), this relative abundance may result from the preservation of forested habitats represented by many of the fossil-bearing strata at Hawk Rim, as well as a temporal transition in the makeup of equid communities across the Hemingfordian-Barstovian boundary. Archaeohippus ulimus is the species described in the region (Downs, 1956); however, other species cannot be ruled out based on the Hawk Rim material. The poorly understood origins of this genus make diagnostic differences between species harder to parse without adequate skull material (O’Sullivan, 2003).

Genus MERYCHIPPUS Leidy, 1858

**Occurrence**—JDNM 267 and JDNM 271.

**Referred Material**—JODA 14976, tooth fragments; JODA 14999, upper molar; JODA 15070, lower molar and two upper molars; JODA 15137, lower molar.

**Description**—Merychippus is the most common equid at most early Barstovian sites, so ample material exists for comparison. Hawk Rim specimens were compared with Merychippus from the Mascall Formation (UCMP 739) and Red Basin (UOMNH F-23322 and UOMNH F-21038). Identification was also facilitated by several distinct features of the genus, such as cementum and increased hypsodonty. These intermediate-sized horses exhibit mesodonty, being higher-crowned than most other coexisting genera (MacFadden, 1999). The lower dentition is unique among Barstovian equids in possessing a moderate to thick layer of cementum on the cheek teeth. Postcranial were difficult to assign to this genus because it is a similar size to parahippine-grade equids such as Desmatippus (Morris, 1965).

**Discussion**—Of all equids present at Hawk Rim, Merychippus is the most difficult to assign to a particular species. Either a much larger sample or complete dentitions would be needed for a species-level assignment. Merychippus is really more of a grade of horses than a genus (Hulbert and MacFadden, 1991). The limited dental material from Hawk Rim suggests that the merychippine-grade horses at the site were different from those in the type Mescal area, Red Basin, or Railroad Canyon, because the teeth are all from much smaller animals than the other sites. However, previous authors have noted the large amount of variation exhibited by this genus (Barnosky et al., 2007); thus, Hawk Rim may only exhibit increased phenotypic variation in response to a more closed environment or the characteristic size of a slightly earlier time period currently not represented in the Oregon fossil record.

Genus DESMATIPPIUS Scott, 1893

**Occurrence**—JDNM 267 and JDNM 271.

**Referred Material**—JODA 14973, lower molar; JODA 14992, tooth fragments; JODA 14996, upper molar; JODA 15025, tooth; JODA 15031, tooth; JODA 15156, upper molar fragment.

**Description**—Like Merychippus, only dental material could be referred definitively to this genus on the grounds of the similar
size and postcranial morphology of the two larger equid genera at the site. Dental material was diagnostic in that it was considerably larger than Archaeohippus material, but was also low-crowned and lacked cementum in the lower molars. Postcranial material could not be assigned to genus because it is similarly sized in Merychippus and Desmatippus.

**Discussion**—Previous publications cite the occurrence of Parahippus and not Desmatippus in the Oregon Barstovian (Downs, 1956; Shotwell, 1968; Fremd, 2010). However, the material known from Oregon in the past, to which these publications referred, was referable to Parahippus avus, a species that has been subsequently transferred to Desmatippus (MacFadden, 1998). Only Parahippus avus has been recorded in the region, thus a generic assignment to Desmatippus in favor of Parahippus is consistent with the faunal record of the region.

**EQUIDAE**, indet.

**Occurrence**—JDNM 267, JDNM 269, JDNM 270, JDNM 271, and JDNM 272.

**Referred Material**—JODA 14967, distal tibia; JODA 14982, tooth fragment; JODA 14985, tooth fragment; JODA 14993, astragalus and phalanx; JODA 14997, tooth fragment; JODA 15019, metapodial and tooth fragment; JODA 15021, astragalus; JODA 15022, calcaneum; JODA 15023, tooth fragments; JODA 15067, tibia fragment; JODA 15096, tooth fragment; JODA 15101, metapodial; JODA 15109, tooth fragment; JODA 15114, astragalus; JODA 15128, tooth fragment.

**Description**—Although all material was clearly equid in nature, this material was all from intermediate-sized equids. Therefore, it was impossible to determine if the postcranial material belonged to Merychippus or to Desmatippus or possibly even large specimens of Archaeohippus. Dental material was too fragmentary in nature to even estimate the overall size of the tooth. All astragali possessed slanted keels and the compact morphology characteristic of equids. They were within documented size variation for both merychippine- and parahippine-grade horses (Morris, 1965).

**Discussion**—Dental material would indicate that the largest equids were generally Merychippus at this site. Therefore, the largest postcranial material likely belongs to this genus. However, the small sample size precludes any statistical analysis of mass variation in equids at the site, and size alone is poor grounds for a generic assignment.

Family RHINOCEROTIDAE Gray, 1821

**Occurrence**—JDNM 267, JDNM 268, JDNM 270, and JDNM 271.

**Referred Material**—JODA 15002, tooth fragment; JODA 15032, tooth fragment; JODA 15072, deciduous tooth; JODA 15077, tooth fragment; JODA 15083, tooth fragment; JODA 15115, tooth fragment; JODA 15120, tooth fragments; JODA 15123, tooth fragment; JODA 15146, tooth fragments.

**Description**—It was only possible to assign dental material to Rhinoceratidae. All dental material from rhinocerotids has thicker enamel than any other animal found at Hawk Rim, or in the region other than proboscids, and shows the presence of perpendicular banding in the enamel (Prothero, 2005). Several fragments also displayed a prominent cingulum. A nearly complete deciduous tooth was identified by the wear pattern on the underside of the tooth where the roots had dissolved. Deciduous dentitions are not phylogenetically distinct between genera known from the region.

**Discussion**—Both Aphelops and Teleoceras are known from the Mascall Formation (Fremd, 2010). However, with the highly fragmentary dental material yielded by Hawk Rim, distinguishing between these genera is impossible.

Order RODENTIA Bowdich, 1821
Family CASTORIDAE Gray, 1821
Genus ANCHITHERIOMYS Roger, 1885
(Fig. 10C)

**Occurrence**—JDNM 267.

**Referred Material**—JODA 15052, incisor.

**Description**—Although preserved material is limited to only a single incisor, the large size and crenulated enamel facilitated the identification. This genus of castorid is much larger than nearly all other contemporaneous Holarctic rodent taxa. Furthermore, the crenulated enamel, with pronounced longitudinal ridges, is a trait only seen in a few taxa, with no other taxon within several million years sharing that trait (Korth and Emry, 1997).

**Discussion**—This taxon’s geographic range has been limited primarily to the Great Plains. Most known occurrences are in Nebraska, with the genus also reported from Texas, Nevada, and possibly Florida (Mörs and Hulbert, 2010). It is an uncommon member of all reported faunas in which it occurs. Hawk Rim represents an extension of the geographic range for the genus.

Family MONOSOAULAX Stirton, 1935
(Fig. 10A,B)

**Occurrence**—JDNM 267 and JDNM 270.

**Referred Material**—JODA 14984, molar; JODA 15030, molar; JODA 15132, molar.

**Description**—Monosau lax is the only previously known castorid in the Mascall Formation (Fremd, 2010). It is very small compared with other members of the family. The cheek teeth are subhypodont, unlike some later genera of the family. Overall shape of the occlusal surface is round to very slightly ovoid (Stirton, 1935). They have strongly pronounced fossettids, which tend to be oriented nearly perpendicular to the axis of the jaw (Shotwell, 1968). There are no secondary fossettids present in the teeth. All three individual teeth recovered are molars and did not come from the same individual, because they were collected from different strata.

**Discussion**—Although Hawk Rim specimens differ in appearance from both M. typicus and M. progressus, which are found nearby, the level of phenotypic variability in castorids makes it difficult to assign the material to species. Without a much larger sample size or more complete specimens, it is impossible to determine if variation is due solely to differences in wear stage or morphological variation between individuals.
labial face remains flat and not convex as in more derived taxa, such as *Hesperogaulus* (Korth, 1999) and *Mylagaulus* (Korth, 2000; Czaplewski, 2012). There is also a distinct concavity on the labial side of the paracone, even in this mid-wear specimen, a character lost in more derived species of *Alphagaulus*, such as *Alphagaulus tedfordi* and *Alphagaulus douglassi* (Calede and Hopkins, 2012a, 2012b). The premolar is two-rooted, with a large, fused posterior root and a smaller anterior root. The roots are closely fused, with no distinction between labial and lingual posterior roots and only a small separation between the anterior and posterior roots. The base of the tooth is well covered in cementum, but the cementum does not extend up to the occlusal surface as in some derived mylagaulids (Korth, 2000).

Preserved postcranial material identified as mylagaulid is limited to a single distal left humerus. Preservation is quite good, and there is no water wear or other damage to the fossil. Consistent with a burrowing rodent, the distal portion of the humerus is broad and quite robust (Barnosky et al., 2007). The epicondylar process is broad and wing-like (Fagan, 1960). The entepicondylar foramen is small and situated above the medial epicondyle.

**Discussion**—Both specimens were found in the same outcrop, in the Carnivore locality, UO 4360. *Alphagaulus vetus* is already known from the late Hemingfordian of the Northwest, occurring at Massacre Lake, in northwestern Nevada. It is also known from the early Barstovian fauna of the Mascall Formation of Oregon (Caled and Hopkins, 2012a), in addition to occurrences in Wyoming and Nebraska (Korth, 2000). The humerus is attributed to *A. vetus* based on its occurrence with the identified P4. There are other mylagaulids known from the Pacific Northwest in the Middle Miocene, including *Hesperogaulus* (a larger and more robust form) and an even larger and more derived mylagaulid that may be *Ceratogaulus* or *Mylagaulus* (Shotwell, 1968; Calede and Hopkins, 2012a), but this specimen is morphologically consistent with *A. vetus*, so the most likely scenario given its spatial proximity to the premolar is that it represents more material of the same taxon.

**Family SCIURIDAE** Gray, 1821

**Genus PROTOSPERMOPHILUS** Gazin, 1930

**Occurrence**—JDNM 267, JDNM 270, and JDNM 272.

**Referred Material**—JODA 14979, calcaneum; JODA 15063, incisor and postcranial material; JODA 15148, metacarpal.

**Description**—Most material consisted of postcranial remains. Identifications were made possible by comparison with modern sciurids (UOMNH R-8398 and UOMNH R-8394). The incisor is robust and has a cross-sectional shape typical of *Protospermophilus*, with the medial portion flatted and the lateral portion convex (Black, 1963). Furthermore, the material is indicative of a larger animal than *Miospermophilus*, the only other ground squirrel known from the mid-Miocene of Oregon.

**Discussion**—The Hawk Rim material is consistent in size with intermediate-sized species of *Protospermophilus*; however, some species overlap closely enough in size to prohibit a positive identification. The material clearly belongs to a sciurid ecologically similar to modern ground squirrels, based on increased spacing of the distal condyles of the femur as well as the overall robustness compared with tree squirrel limb bones. The limb fragments included in JODA 15063 bear evidence of rodent gnawing prior to burial.
CONCLUSION

Although relatively incomplete vertebrate fossils have been recovered from Hawk Rim, enough material has thus far been generated to facilitate ecological inferences and to allow comparisons with the faunal assemblages of other sites. The assemblage is indicative of a wet, forested paleoenvironment and, taken as a whole, describes the changing ecology of the site through the limited time span represented. Many taxa, including nearly all carnivore material, were recovered from paleosols and therefore certainly represent the fauna present at the site during deposition of sediments and continued development of the soil. The ecological differences at Hawk Rim are important to note in the context of comparing Hawk Rim with other Middle Miocene fossil localities. Hawk Rim’s fauna maintains some faunal components in common with the Mascall type area, Red Basin, and other sites, yet contains distinct faunal components as well. These unique faunal components likely arise from the combination of a slightly earlier time period and ecological heterogeneity across the geographic distribution of the Mascall Formation.

Many, but not all, of these taxa are shared with early Barstovian sites in the region. As a late Hemingfordian site, the Hawk Rim fauna extends several key Barstovian taxa into the earlier section of the Arikareean. Far fewer taxa inhabit the Mascall and significantly smaller than all material from Red Basin. Without more complete material, as well as a larger sample size, the morphological variation derived from species differences or environmentally driven phenotypic plasticity is difficult to tease out. Morphological differences are noted in other taxa as well. The *Dromonemeryx* and oecodont material from Hawk Rim is also notably smaller than that preserved at Red Basin. However, one taxon does prove to be an exception. The single *Moropus* tooth from the site is larger than any other recorded sample from that genus. Because this taxon is not found in Barstovian or Hemingfordian localities proximally, comparisons are impossible, other than noting that it is larger than older samples from the early Hemingfordian parts of the John Day Formation. Also remarkable in Hawk Rim’s fauna is the diversity of Carnivora, in spite of the relatively small fossil sample. With three canids, a felid, a new mustelid, and an amphicyonid, the ungulate fauna clearly supported a diverse array of predatory mammals. These carnivores also illustrate the complex assemblage of biostatigraphy in mid-Miocene carnivores, with typical late Hemingfordian forms represented by *Amphicyon frenensis* and *Pseudaelurus skinneri* and elements of the early Barstovian faunas appearing early in the form of *Tephronyx rurestris* and *Paratormarcus tenerarius*. The discovery of this first late Hemingfordian fauna in Oregon adds to the Massacre Lake site in Nevada to show us a late Hemingfordian fauna and the rise of the Pacific Northwest’s characteristic diverse mid-Miocene fauna and the evolution of ecology in this tectonically active landscape.

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